

The brain in flow: a systematic review on the neural basis of the flow state

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1 **Abstract**

2 **Background:**

3 Flow state is a subjective experience that people report when task performance is
4 experienced as automatic, intrinsically rewarding, optimal and effortless. While this intriguing
5 phenomenon is the subject of a plethora of behavioural studies, only recently researchers have
6 started to look at its neural correlates. Here, we aim to systematically and critically review the
7 existing literature on the neural correlates of the flow state.

8 **Methods:**

9 Three electronic databases (Web of Science, Scopus and PsycINFO) were searched to
10 acquire information on eligible articles in July, 2021, and updated in March, 2022. Studies that
11 measured or manipulated flow state (through questionnaires or employing experimental
12 paradigms) and recorded associated brain activity with electroencephalography (EEG),
13 functional magnetic resonance (fMRI) or functional near-infrared spectroscopy (fNIRS) or
14 manipulated brain activity with transcranial direct stimulation (tDCS) were selected. We used
15 the Cochrane Collaboration Risk of Bias 2 (RoB 2) tool to assess the methodological quality
16 of eligible records.

17 **Results:**

18 In total, 25 studies were included, which involved 471 participants. In general, the
19 studies that experimentally addressed flow state and its neural dynamics seem to converge on
20 the key role of structures linked to attention, executive function and reward systems, giving to
21 the anterior brain areas (e.g., the DLPC, MPFC, IFG) a crucial role in the experience of flow.
22 However, the dynamics of these brain regions during flow state are inconsistent across studies.

23 **Discussion:**

24 In light of the results, we conclude that the current available evidence is sparse and
25 inconclusive, which limits any theoretical debate. We also outline major limitations of this
26 literature (the small number of studies, the high heterogeneity across them and their important
27 methodological constraints) and highlight several aspects regarding experimental design and
28 flow measurements that may provide useful avenues for future studies on this topic.

29

30 **Keywords:** consciousness, cognitive processing, phenomenology, EEG, fMRI, tDCS, fNIRS

31

32 1. Introduction

33 Have you ever been so focused on a task that you stopped noticing what was going on
34 around you? Were you exercising, playing an instrument or working and felt that it took less
35 effort than usual, or that time flew by? If so, then you have experienced what Csikszentmihalyi
36 (1975) called “flow state”, a subjective experience in which the person is absorbed in the task
37 and action seems to occur smoothly and automatically. The interest in this phenomenon has
38 resulted in a wealth of literature investigating its subjective and behavioural manifestation (e.g.,
39 Csikszentmihalyi, 2020; Ottiger et al., 2021; Swann et al., 2012), albeit much less research has
40 been conducted to pinpoint its neural signatures. Here, we systematically review the extant
41 evidence on the neural correlates of flow state from a critical perspective, highlighting both the
42 advances in the field and what we consider major limitations.

43 Investigating the flow state, also known as "being in the zone", has theoretical and
44 practical relevance. At the theoretical level, flow state has been described as a particular state
45 of consciousness, related to core cognitive processes such as vigilance and attention
46 (Csikszentmihalyi et al., 2021). On a practical level, the state of flow has long raised the
47 attention of researchers because of its potential role in linking feelings of enjoyment and
48 subjective well-being, with optimal cognitive and physical performance (e.g., Flett, 2015;
49 Khoshnoud et al., 2020). For instance, in a 10-year longitudinal study in which over 5000
50 executives were asked about their flow experiences at work, Cranston and Keller (2013)
51 showed that people in flow state reported increasing their productivity by 500%. An
52 improvement in performance associated with the flow state has also been observed in other
53 contexts, such as sports (e.g., Stavrou et al., 2007) and music (e.g., MacDonald et al., 2006).

54 When defining the flow state, the majority of studies based on subjective measures (e.g.,
55 questionnaires or verbal reports) agree on the following nine dimensions (e.g., Nakamura and
56 Csikszentmihalyi, 2014): 1) clear goals, 2) high level of concentration on the task, 3) balance
57 between the individual's skills and task difficulty, 4) immediate feedback about performance,
58 5) sense of control, 6) fusion of action and consciousness or automaticity, 7) autotelic property
59 or intrinsically rewarding activity, 8) changed experience of time, and 9) decreased self-
60 consciousness and absence of worry. In addition to these classical experiential factors, certain
61 facilitating conditions seem also necessary for the flow state to arise (e.g., Lambert and
62 Csikszentmihalyi, 2020). In general, the state of flow is usually experienced by highly
63 motivated experts (e.g., surgeons) with traits of autotelic personality, carrying out critical tasks

64 (e.g., a surgery) in well-known task-related scenarios (e.g., operating room) during prolonged
65 periods of time without interruption.

66 Even if anyone can achieve a state of flow when the conditions described above (e.g.,
67 balance between difficulty and skill) are met, there are individual differences in the
68 ease/frequency with which people enter this state (Schmidt et al., 2014). Overall, current
69 evidence suggests that differences in the tendency to experience flow may be determined by
70 autotelic personality traits (Ross & Keiser, 2014), genes associated with the neurotransmitter
71 dopamine receptors (Gyurkovics et al., 2016), and social and educational factors (Heo et al.,
72 2010). High self-esteem, low neuroticism, high extraversion, higher school support, higher
73 employment status, higher availability of D2R in the striatum and CC homozygotes of the
74 DRD2 C957T SNP gene are associated with more frequent experiences of flow (Butkovic et
75 al., 2015; de Manzano et al., 2013; Gyurkovics et al., 2016; Heo et al., 2010; Mosing et al.,
76 2012; Ullén et al., 2016). In fact, Mosing and collaborators (2012) estimated a heritability of
77 41% for general flow proneness. Paradoxically, even if all the above conditions are met in a
78 person who is prone to experiencing flow, flow state does not necessarily arise. Eliciting and
79 capturing the flow state therefore seem rather elusive, even more so in controlled laboratory
80 conditions (e.g., with an individual inside the functional magnetic resonance imaging –fMRI–
81 scanner). Nevertheless, researchers have attempted to investigate the neural basis of flow.

82 In search of the neural correlates of flow state, several brain systems and networks have
83 been pointed out as potential neural underpinnings of this experience (see van der Linden et al.,
84 2021, for a brief summary): a) the reward system, a mesocorticolimbic circuit which includes
85 amygdala, hippocampus, nucleus accumbens, and ventral diencephalon (e.g., hypothalamus),
86 as well as cortical areas (e.g., dorsolateral prefrontal and cingulate cortices, the insula),
87 critically involved in positive or negative reinforcement and motivation processes (Makris et
88 al., 2008); b) attentional networks, such as the orienting network —related to the selection of
89 targets towards which the attentional focus is directed, and that includes the superior parietal
90 cortices, the temporal-parietal junction and the frontal eye fields (Posner & Rothbart, 2007)—
91 and the alerting network —associated with the increases and maintenance of the attentional
92 level, and that includes the locus coeruleus and right frontal and parietal cortices (Posner &
93 Rothbart, 2007)—; and c) the default mode network, a complex set of brain regions (i.e.,
94 anterolateral middle temporal cortex, posteromedial cortex, angular gyrus, inferior frontal
95 gyrus and medial prefrontal cortex) involved in both resting and mind-wandering states, as well

96 as in higher-order cognitive processes (e.g., decisions based on internal rules; Smallwood et
97 al., 2021). These neural systems seem to be involved in some of the conditions traditionally
98 associated with the state of flow, such as its autotelic property, high levels of concentration and
99 attention, or the influence of previous experiences. The fundamental question hence is whether
100 the current evidence provides solid support for the involvement of any of these networks, or
101 any other brain regions in the generation of the flow experience.

102 The findings of the studies searching for the neural basis of flow have been traditionally
103 framed along with two main theoretical accounts: the Transient Hypofrontality Hypothesis
104 (THH; Dietrich, 2004) and the Synchronization Theory of Flow (STF; Weber et al., 2009).
105 According to the former, flow state requires the support of implicit and automatic systems,
106 including the basal ganglia and cerebellum, as well as the inhibition of most cognitive functions
107 linked to prefrontal areas (considered more explicit systems; Dietrich, 2004). On the other
108 hand, the STF, based on Posner's (1987) tripartite attentional model, suggests that flow state
109 arises from the synchronization of focused attention networks (alertness and visual orienting
110 networks) together with the striatal reward networks, whose activation would allow the
111 pleasurable component of flow state to rise. Very recently, in an attempt to reconcile these two
112 seemingly opposite explanations of the flow state, Gold and Ciorciari (2021) developed a more
113 comprehensive neural model of flow: the Internal Model of Flow. According to this framework,
114 the underlying neural mechanism of flow state relies on internal models formed in the
115 cerebellum during the acquisition of cognitive or motor skills. When an individual is
116 experiencing flow, the orders to execute the actions would come, in first place, from frontal
117 areas (e.g., the premotor cortex, the pre-supplementary motor cortex or the anterior cingulate
118 cortex). These instructions, instead of being executed by the prefrontal cortex (if the task is
119 cognitive) or the motor cortex (if it implies physical activity), would be carried out by the
120 cerebellum when in flow. This cerebellar control would be responsible for the experience of
121 intuitive and effortless behaviour. Thus, a secondary question addressed by the present paper
122 would be to explore whether current research on the neural basis of flow provides support for
123 any of these theoretical models.

124 The aim of the present systematic review is to synthesise and organise the current
125 evidence on the neural correlates of flow state. To this end, we searched for studies using
126 neuroimaging techniques such as electroencephalography (EEG), fMRI or functional near-
127 infrared spectroscopy (fNIRS) to measure brain activity, and transcranial direct current

128 stimulation (tDCS) to modulate neural activity while inducing or assessing the experience of
129 flow. The results are critically summarized considering the latest theoretical accounts of the
130 flow state, the shortcomings of the investigation up to now, and what, in our opinion, are key
131 methodological issues to address by future research.

132

133 **2. Methods**

134 This systematic literature review followed the Preferred Reporting for Items for
135 Systematic Reviews and Meta-Analyses (PRISMA) guidelines (Moher et al., 2015).

136 *2.1. Literature search*

137 In July 2021, and again in March 2022 (to update the search after the first round of
138 reviews), the electronic databases Web of Science (main collection), Scopus and PsycINFO
139 were searched for relevant studies by a string that combined the following terms: ("flow stat*"
140 OR "flow experienc*" OR "experienc* of flow" OR "stat* of flow" OR "flow engagement"
141 OR "flow-like stat*" OR "psychological flow" OR "theory of flow" OR "cognitive flow" OR
142 "being in the zone" OR "flow research") AND (EEG OR fMRI OR tDCS OR TMS OR FNIRS)
143 NOT ("optic flow" OR "current flow" OR "airflow"). The literature search was narrowed to the
144 title, abstract or keywords of original published studies written in English language. Additional
145 titles were identified by a manual search of reference sections of topic-relevant papers and
146 citations to them by other papers.

147

148 *2.2. Eligibility criteria*

149 Studies were considered eligible for inclusion if they met the following criteria: (a)
150 studies that measured or manipulated flow state (through questionnaires or employing
151 experimental paradigms) and recorded associated brain activity; (b) peer-reviewed papers or
152 preprints with a DOI. Exclusion criteria were: (a) exploratory studies that did not measure brain
153 activity during the flow state; (b) systematic or narrative reviews on the psychophysiology of
154 the flow state; (c) studies with clinical samples. We did not establish any restrictions on
155 publication date.

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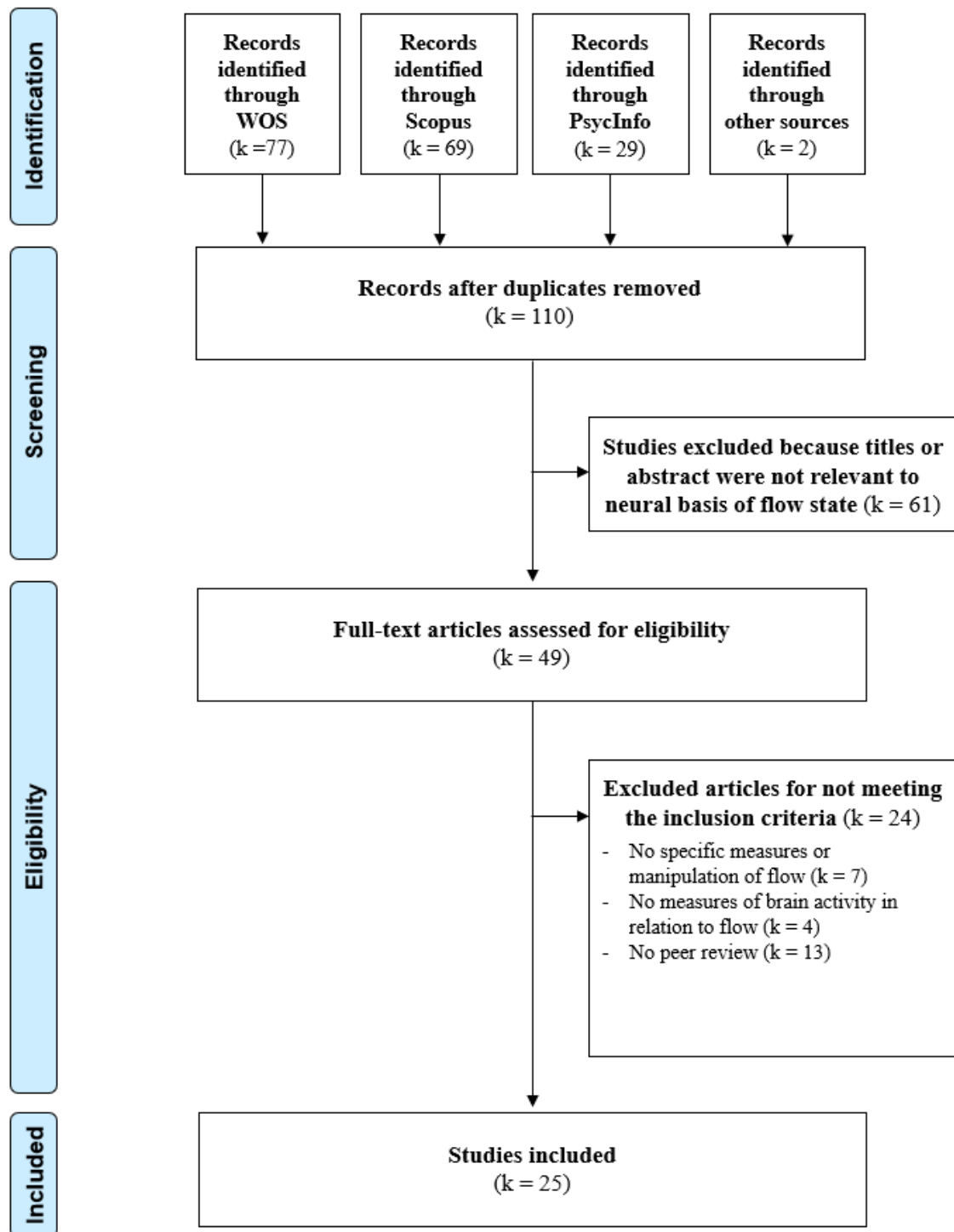
157 *2.3. Study selection*

158 After conducting electronic database searches, we pooled results and removed duplicate
159 articles by using Mendeley software. Next, articles with irrelevant titles and abstracts were
160 excluded. Then, the excluded articles were examined by the last author (LC) to double-check
161 their relevance for this review (none of the excluded articles was included again in the pool of
162 relevant studies). The first (CA) and the last author (LC) assessed and judged independently
163 the full texts of potentially relevant studies with respect to eligibility (see flowchart in Fig. 1
164 for details; see Excluded studies, in Supplementary material for details, i.e., references and
165 reasons for exclusion). In case of disagreement, as was the case for 4 articles, the second author
166 (DS) was consulted to reach a consensus.

167 Relevant information from all the included studies was retrieved by the first author
168 using a data extraction table form developed a priori (see Table 1). Extracted data include: (i)
169 characteristics of the study sample; (ii) experimental paradigm used; (iii) flow measures; (iv)
170 brain activity technique; (v) main findings.

171 *2.4. Risk of bias*

172 A slightly modified version of the RoB 2 tool (revised Cochrane risk of bias tool for
173 randomised trials; Sterne et al., 2019) was used to estimate the risk of bias in the 25 selected
174 studies (see Risk of bias, in Supplementary material).



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Figure 1. PRISMA flow chart for study inclusion

177 3. Results

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Our initial search, which was carried out for the first time in July 2021, yielded 122 eligible records. The search in March 2022 resulted in the inclusion of 55 further studies, resulting in a total of 177 eligible records (see Fig. 1). Then, we eliminated 67 duplicate records.

181 From the remaining 110 studies, we excluded 61 studies non-related with the neural correlates
182 of flow state or reviews about this topic, and 24 because they did not fulfil eligibility criteria
183 (see figure 1, for details). Finally, 25 studies were included in this systematic review.

184

185 **3.1. Research on cerebral blood flow: fMRI and perfusion MRI**

186 Within the studies included in this systematic review, there are 7 studies that used
187 neuroimaging techniques (fMRI and perfusion) to measure brain activity while (trying to)
188 inducing flow state through different experimental protocols (Ju and Wallraven, 2019; Klasen
189 et al., 2012; Huskey et al., 2018a; Huskey et al., 2018b; Ulrich et al., 2014; Ulrich et al., 2016a,
190 2016b).

191 *Difficulty-based studies*

192 The best example of this approach is the landmark study conducted by Ulrich and
193 collaborators (2014) employing a mental arithmetic task to induce flow in 27 healthy male
194 adults while recording their brain activity with fMRI. Participants were instructed to perform
195 sums varying in difficulty. The difficulty was manipulated by adding or removing one –or
196 two– digit numbers in the incoming operation to create 3 different experimental conditions
197 where the difficulty of the sums could be a) excessively easy compared to the participant's
198 skills level: the “boredom condition” (as it was not challenging enough and, therefore, flow
199 was unlikely to emerge); b) excessively difficult compared with the participant’s skills: the
200 “overload condition”; c) dynamically adjusted to participant’s ongoing performance: the “flow
201 condition”. Three blocks of each condition (lasting 184 seconds each) were performed in a
202 random order. After each block, participants completed 9 Likert-scaled flow-related items to
203 assess their subjective experience (desire to solve calculations again, feeling involved, thrilled,
204 bored, or focused, having the necessary skills, ability-difficulty balance, number of task-
205 relevant thoughts, and subjective time experience). The results revealed increased cerebral
206 blood flow in the left inferior frontal gyrus (IFG) and putamen, as well as in posterior cortical
207 regions during what they called flow condition, relative to the boredom and overload
208 conditions. In addition, they report reduced activity in the medial prefrontal cortex (MPFC)
209 during flow state compared with overload and boredom conditions. Interestingly, they found
210 that the neural activity in the IFG and the amygdala correlated with the subjective experience
211 of flow. The authors suggest that the relative increase of neural activity found in the IFG which

212 correlated with the subjective experience of flow might be associated with a high sense of
213 control during the task, one of the main features of the flow state. However, increased activity
214 in the IFG has been also associated with mental arithmetic solving (e.g., Arsalidou and Taylor,
215 2011; Baldo and Dronkers, 2007; Zago et al., 2008), especially when task difficulty is high
216 (e.g., Gruber et al., 2001; Kong et al., 2005). On the other hand, the authors point to arousal as
217 a potential mechanism responsible for the reduced activity found in the amygdala, which may
218 reflect a decreased arousal level during flow state (e.g., Lewis et al., 2007; McGaugh, 2004),
219 although it would not explain why it was different from the boredom condition which should
220 also be associated with even lower arousal.

221 Although these results were partially replicated in a subsequent experiment by the same
222 authors (Ulrich et al., 2016a, 2016b), several methodological issues compromise the validity
223 of these findings. Firstly, this paradigm is based exclusively on one of the 9 flow dimensions:
224 skills-difficulty balance. That is, it is inferred that the flow state will naturally arise in a
225 situation in which the difficulty of the task (i.e., performing sums) and the mathematical skills
226 of the subject are balanced. However, the complex nature of flow state implies that it does not
227 necessarily emerge in situations where skills and task difficulty are balanced (i.e., skills-
228 difficulty match is a necessary condition but not sufficient). Other key factors such as autotelic
229 ownership or intrinsically rewarding activity seem necessary for the flow state to emerge
230 (Nakamura & Csikszentmihalyi, 2009). Secondly, performing sums is perhaps not as
231 intrinsically rewarding as other tasks (i.e., playing video games). Thirdly, the flow experience
232 appears to emerge while engaged in tasks lasting longer than 3-min (Csikszentmihalyi, 2020).
233 Thus, performing a mathematical task —often associated with negative emotions in students
234 (Lewis, 2013)— for blocks of such short duration (184 seconds) does not seem the ideal
235 scenario for inducing flow state. Fourthly, the experimental sessions were carried on in an MRI
236 scanner, an unusual, claustrophobic and noisy situation for most people which would definitely
237 hinder the likelihood of experiencing flow. Lastly, in addition to the methodological limitations
238 more closely related to the induction of the flow state, the results of these studies could have
239 been also undermined by a notable risk of bias (e.g., significances were not corrected for
240 multiple comparisons; see Risk of bias, in Supplementary material).

241 *Dual-task studies*

242 Huskey and collaborators (2018b, 2018a) followed a different approach to explore the
243 neural correlates of flow state using a dual-task paradigm. This approach would eventually lead

244 to two separate articles with different levels of analysis of brain activity (Huskey, Craighead,
245 et al., 2018; Huskey, Wilcox, et al., 2018). In that experiment, 18 healthy young participants
246 were required to play an experimental video game with three difficulty conditions (i.e., low,
247 balanced and high), each lasting for 120s, while performing a secondary visual reaction time
248 (RT) task. In line with their hypotheses, participants reported higher intrinsic reward sensitivity
249 (using the autotelic personality subscale of the Activity Experience Scale; Jackson and Eklund,
250 2002) in the balanced-difficulty condition (considered as flow condition based on the same idea
251 as the arithmetic task in which skills-difficulty balance implies the emergence of flow state)
252 compared with low and high difficulty conditions. In addition, they found higher RT in the
253 secondary task during the balanced-difficulty condition relative to the high and low difficulty
254 conditions (Huskey, Craighead, et al., 2018). Interestingly, these behavioural results were
255 accompanied by increased activity in structures associated with cognitive control like the
256 dorsolateral prefrontal cortex (DLPFC), the visual orienting and alertness attentional networks
257 (i.e., superior parietal lobe and dorsal anterior insula, respectively); as well as structures of the
258 reward system (i.e., putamen) in the balanced condition compared to the low and high difficulty
259 conditions, as recorded with fMRI. Subsequent analyses of this database (Huskey, Wilcox, et
260 al., 2018), revealed no greater brain connectivity between cognitive control and reward brain
261 networks during the flow condition compared with the easy and difficult conditions. Further,
262 they explored whether the skills-difficulty balanced condition (i.e., flow condition) was
263 associated with an energetically-efficient topology (as characterized by connections between
264 nodes within a network). In line with their prediction, the flow condition was associated with
265 a lower brain efficiency score (see Rubinov and Sporns, 2010, for a comprehensive explanation
266 of this measure) than the other difficulty conditions, which is interpreted as an index of lower
267 energetic cost.

268 Since flow state implies focus and full immersion into a primary task, evaluating the
269 performance of a secondary simultaneous task, which should be poor when flow emerges,
270 seems a reasonable way to assess to which extent an individual is experiencing flow. In that
271 sense, the dual-tasking approach may provide an alternative way to explore the behavioural
272 and neural correlates of flow. However, the experiment conducted by Huskey and collaborators
273 (Huskey, Craighead, et al., 2018; Huskey, Wilcox, et al., 2018) is based again on the implicit
274 (and likely erroneous) premise that flow state will necessarily arise if task's difficulty and
275 individual's skills are balanced. Moreover, flow state was not directly measured. Although the
276 authors assessed the participants' intrinsic reward sensitivity, it represents only a single,

277 necessary but not sufficient, feature of a situation prone to trigger a flow state. Therefore, the
278 dual-tasking experimental paradigm implemented in this study does not allow one to draw
279 conclusions on whether those increases in RT and the associated changes in brain activity were
280 due to the actual presence of flow state or to mere attentional dynamics while performing tasks
281 varying in difficulty.

282 *Video games studies*

283 Video games have been frequently used in experimental research to address flow state
284 (Michailidis et al., 2018). This approach is based on the premise that immersive enjoyable
285 video games would be associated with higher chances of triggering flow experiences compared,
286 for example, with performing sums. However, the combination of video games and fMRI has
287 been implemented only two times. In a pioneering study, Klasen and collaborators (2012) asked
288 13 regular video game players to play a first-person shooter video game while recording their
289 brain activity with fMRI. Researchers analysed the content of the game and classified
290 (according to their subjective criteria) which situations were more related to some of the
291 dimensions of flow (e.g., skills-difficulty balance, focus, clear goals, and control over the
292 situation) in order to identify the moments with higher probability of experiencing flow. During
293 those flow-like situations, increased activity in sensorimotor brain networks (i.e., left primary
294 and secondary somatosensory cortex and motor areas) and the cerebellum was observed. A
295 latter fMRI study (Ju & Wallraven, 2019) addressed flow state by using a similar video game
296 approach in 31 healthy young participants, finding increased activity in areas involved in the
297 default mode network. Nevertheless, the experimental design of these studies is undermined
298 by the same methodological constraints of the previous reports (e.g., the absence of flow
299 measures, manipulating flow by modifying difficulty level). It should be noted, for example,
300 that investigating the situations with an enhanced likelihood of flow is not equivalent to
301 measuring the flow directly. Likewise, finding activity changes in brain areas related to
302 cognitive processes does not necessarily mean they are linked to flow experience, since an
303 individual can be totally focused on a task and perform well without experiencing flow state.
304 Thus, the brain patterns found in these studies cannot be directly attributed to flow state.

305 In sum, even if some of the fMRI studies report changes in brain areas and neural
306 systems that might be, in theory, related to flow state, several methodological issues raise
307 doubts about the validity of these findings (i.e., whether the observed brain correlates might be
308 actually attributable to the experience of flow).

310 **3.2. Research on oxygen concentration: fNIRS**

311 fNIRS is another non-invasive neuroimaging technique to measure cerebral
312 hemodynamic with a high temporal resolution. Note that, although this technique seems
313 particularly pertinent in flow research since it is especially useful to measure prefrontal cortex
314 activity, which has been repeatedly pointed as a key system in the experience of flow (e.g.,
315 Dietrich, 2004; Weber et al., 2009), fNIRS does not allow to assess the activity of the striatal
316 reward networks, which is another important component of flow state according to the
317 Synchronization Theory of Flow (Weber et al., 2009). We identified 5 studies addressing the
318 neural correlates of flow by means of fNIRS (de Sampaio Barros et al., 2018; Harmat et al.,
319 2015; Hirao, 2014; Yoshida et al., 2014; Yu et al., 2022).

320 Three of these studies (de Sampaio Barros et al., 2018; Harmat et al., 2015; Yoshida et
321 al., 2014) implemented the same experimental paradigm, instructing a set of participants to
322 play the classic Tetris video game in different difficulty conditions (modulated by the speed of
323 the game). By relying on the skills-difficulty balance, they inferred that a difficulty-adjusted
324 condition would trigger a flow state. Indeed, in all of these three studies, the self-reported
325 experience of flow state was higher for the difficulty-adjusted condition compared with the
326 low-difficulty condition; however, their results were mixed. On one hand, Yoshida et al. (2014)
327 and de Sampaio Barros et al. (2018) reported increased activity in the prefrontal cortex during
328 the adjusted-difficulty (i.e., flow) condition compared with the low-difficulty (i.e., boredom)
329 condition in 15 and 20 young participants, respectively. On the other hand, Harmat and
330 collaborators (2015) found no association between prefrontal cortical oxygenation and flow
331 using the same video game in a sample size of 35 university students.

332 Similarly, Yu et al. (2022) recently manipulated the level of difficulty of a music game
333 to induce flow states in regular video game players and people with no video game experience,
334 while measuring prefrontal lobe activity with fNIRS. According to their findings, flow ratings
335 correlated linearly with the increase in oxygenated hemoglobin concentration level in
336 prefrontal areas (DLPFC and frontal pole area) in regular and non-regular players. The results
337 from these four studies contrast with the findings reported by Hirao (2014) using a verbal
338 fluency task. In that study, flow experience of 60 young adults was positively correlated with
339 prefrontal hemodynamic suppression.

340 This set of studies is particularly relevant for the theoretical debate on the neural
341 mechanisms underlying flow state because they directly tested the THH proposed by Dietrich
342 (2004). In fact, three of the five studies reviewed here showed increased activity in prefrontal
343 regions, which would be contrary to what is proposed by the THH. Nevertheless, it is important
344 to note that these findings are undermined by the same issues of previous studies using fMRI,
345 plus potential biases associated primarily with the measurement of brain activity or the
346 selection of reported results (see Risk of bias, in Supplementary material). Thus, we cannot
347 rule out the THH based on these findings.

348

349 **3.3. Research on neural oscillations: EEG**

350 We identified 11 studies addressing the neural correlates of flow with EEG (4 were case
351 studies) while trying to induce flow state through different experimental protocols (Farrugia et
352 al., 2021; Katahira et al., 2018; Knierim et al., 2018, 2021; Leroy & Cheron, 2020; Moreno et
353 al., 2020; Núñez Castellar et al., 2019; Shehata et al., 2021; Wolf et al., 2015; Wollseiffen et
354 al., 2016; Yun et al., 2017).

355 *Difficulty-based studies*

356 The study of Katahira and collaborators (2018) is particularly relevant as it has
357 attracted the most attention (according to the number of citations) from the scientific
358 community interested in flow state. They employed the arithmetic task developed by Ulrich et
359 al. (2014) in order to induce flow state in 16 participants. After performing the arithmetic task
360 in the three difficulty levels (i.e., low, adjusted and high), participants self-reported their
361 experience of flow. As expected, the subjective ratings of flow state were higher for the
362 adjusted-difficulty condition (i.e., the so-called flow state condition) compared with the easier
363 (i.e., boredom) and difficult (i.e., overload) conditions. Notably, the authors found higher theta
364 power in frontal electrodes during flow and overload conditions, relative to the boredom
365 condition. The authors suggest that the higher activity of theta might be related to the high
366 cognitive control demands required by the task in the flow and overload condition. On the other
367 hand, they found increased alpha power during the flow condition compared with the boredom
368 condition (i.e., low difficulty), that they attributed to the difficulty level of the task, since they
369 also found higher alpha power in the overload condition (i.e, high difficulty) relative to the
370 flow condition (i.e., moderate difficulty). In a similar vein, Knierim and collaborators (2018)

371 by using the same arithmetic task ($n = 7$) pointed to alpha and theta brain rhythms at fronto-
372 central locations as potential brain correlates associated with flow state. Very recently, these
373 same authors (Knierim et al., 2021) evaluated the usability of an portable EEG system —Brain-
374 Computer-Interface (OpenBCI) platform with c-shaped EEG electrode array (cEEGrid)—
375 while 6 participants performed the same mathematical task, and found that, again, more intense
376 subjective flow experiences were associated with moderate levels of alpha activation in
377 temporal areas. Thus, different studies using arithmetic tasks agree in pointing to alpha as the
378 power band associated with flow state. The authors suggest that alpha activity could be
379 involved in a relatively moderate working memory load (Katahira et al., 2018), in sustained
380 attention processes (Knierim et al., 2018), or in a reduction of neural activity due to an efficient
381 use of analytical-verbal reasoning during flow state (Knierim et al., 2021).

382 *Dual-task studies*

383 Dual-task paradigms have also been used to explore the neural correlates of flow using
384 EEG. As aforementioned, this paradigm is based on the hypothesis that the more attention
385 devoted to the primary task, the less attention will be available for the secondary task, which
386 should result in longer RTs. In line with this hypothesis, Núñez-Castellar and collaborators
387 (2019) asked 18 participants to perform a classic auditory oddball task while playing a video
388 game in three difficulty conditions (i.e., low, adjusted and high), after which the subjects had
389 to answer two questionnaires on flow experience. The authors assumed, as in most of the
390 research on this topic, that skills-difficulty balance would lead participants to a flow state. The
391 results revealed a lower amplitude of the P300 (i.e., an event-related positive deviation of
392 voltage traditionally linked to attentional and executive processes; Polich and Kok, 1995)
393 elicited by the oddball stimulus in central electrodes during the difficulty-adjusted condition
394 (i.e., flow condition) compared with the low (i.e., boredom) and high (i.e., overload) difficult
395 conditions. The authors suggest that the lower amplitude of P300 during flow condition may
396 indicate that subjects were paying less attention to the secondary task, which may be an indirect
397 marker of flow state. In addition, they found increased alpha power in frontal electrodes during
398 the flow condition compared with boredom and overload conditions, which also correlated with
399 longer RTs in the secondary task.

400 A similar dual-task paradigm was used by Yun and collaborators (2017) to address the
401 EEG correlates of flow state. In this study, 29 healthy young participants were instructed to
402 play a first-person shooting game (primary task) while a sequence of auditory tones was

403 randomly presented across time (secondary task). They were asked to ignore these game-
404 unrelated tones while playing during 60 minutes divided into two blocks of 30 minutes varying
405 in difficulty (low and high). Then, participants retrospectively rated their performance and
406 identified periods of flow state and non-flow state (the average duration of flow was $8.31 \pm$
407 3.61 min; 13.9% of total time). The results revealed a lower increase of beta band power evoked
408 by the tones (secondary task) in the anterior cingulate cortex during flow state compared with
409 non-flow state. In addition, this suppressed beta power correlated positively with the self-
410 reported experience of flow. Despite this study is still a preprint, it represents a well-focused
411 approach to study flow state in a laboratory since they used an intrinsically motivating task
412 (first-person video game) to facilitate flow emergence while testing the neural response to a
413 secondary (irrelevant) task, with (relatively) long periods of time without interruptions, a high
414 density EEG system (128 channels) and a relatively high sample size (i.e., 29 participants) with
415 previous experience with video games (average 13.6 ± 10.1 hours/week).

416 *Exercise-related studies*

417 Sport or physical activity has also been used to induce flow state while collecting EEG
418 activity. The first exercise-based approach to the EEG correlates of flow was conducted by
419 Wolf and collaborators (2015). They recruited a set of amateur ($n = 15$) and expert table tennis
420 players ($n = 14$), who performed a task of observation and mental imagery of motor actions.
421 Participants were instructed to observe 40 videos of table tennis serves, imagining that the score
422 was 10-10 (next point would win the match) and that they had to react to that serve. The flow
423 state was measured after the task using a short questionnaire (Flow Kurz Scala; Rheinberg et
424 al., 2003). The authors found that, in the early instances of movement execution, elite players
425 showed higher asymmetry between hemispheres in temporal lobe activity (i.e., higher activity
426 in the temporal lobe of the right hemisphere compared to the temporal lobe of the left
427 hemisphere) relative to the amateurs, which was associated with a greater self-reported
428 experience of flow. They suggest that this pattern of neural activity may indicate a suppression
429 of analytical-verbal activity and irrelevant cognitive processes during the flow state, as well as
430 greater psychomotor efficiency in elite athletes compared to amateurs.

431 In our view, Wolf and collaborators' (2015) conclusions cannot be drawn from this
432 experiment for several reasons. Firstly, half of the expert participants reported low levels of
433 flow experience (i.e., 7 participants scored below 5 in the 7-point self-rating flow scale) which
434 may cast doubt on whether subjects were actually experiencing flow. Secondly, the many

435 differences between elite players and amateurs when faced with a table tennis task even in
436 imagination (e.g., previous experience with similar situations, highly trained motor reactions,
437 opponent movement prediction/anticipation, fitness, etc.) do not allow attributing the observed
438 neural changes to an experience of flow or simply to any of the other between group
439 differences.

440 Another exercise-related approach was led by Wollseiffen and collaborators (2016),
441 using a dual-task paradigm that combined a primary exercise task (ultramarathon) and a
442 secondary task (arithmetic problem solving). A group of 11 experienced ultramarathoners
443 performed six consecutive 1-hour periods of run, between which EEG (portable device), mood,
444 and cognitive performance measures were collected. These measures were also obtained before
445 and after the 6-hour run. Their results revealed that self-reported flow levels increased after
446 one hour of running and decreased between the first and third hour, remaining relatively stable
447 for the rest of the race. This transient dynamic of flow was not followed by the activity of beta
448 brain rhythm, which decreased after the first hour and remained stable throughout the rest of
449 the race. The authors attribute this phenomenon to a floor effect, suggesting that the activity of
450 the prefrontal cortex during exercise reached its lowest level after the first hour. Notice that
451 there was no correlation between the individual experience of flow and the decrease in frontal
452 beta activity. In addition, they found an increase in global alpha activity after the first 4 hours.
453 Notably, performance in the secondary task did not change over time.

454 In our opinion, the exercise-based studies described above might be considered
455 (together with the video game studies) among the best approaches to study flow state to date.
456 Physical activity, in particular long-lasting activities such as an ultramarathon, are especially
457 suitable to trigger experiences of flow since they are intrinsically rewarding activities prone to
458 automaticity, performed by highly motivated experts (in those studies), during prolonged
459 periods of time, with clear goals and immediate feedback about performance. However, there
460 are many methodological caveats that diminish the extent to which their findings can be
461 explained by a state of flow or, in contrast, by the physical activity itself (e.g., reliability of
462 low-density portable EEG system, poor signal-to-noise ratio, absence of a proper control
463 condition).

464 *Case studies*

465 Another way of trying to investigate the oscillatory brain dynamics of flow state is
466 through case studies, in which researchers usually work with highly experienced individuals in
467 a particular task (i.e., individuals who like the task, know very well their skills and can
468 experience a high sense of control of the situation and task performance), which would
469 facilitate the emergence of flow state. Furthermore, case studies provide an opportunity to
470 collect (neural) data in ecological contexts and a fine-grained characterization of the flow
471 experience. We identified 3 relevant case studies using this approach (Farrugia et al., 2021;
472 Leroy & Cheron, 2020; Moreno et al., 2020). In general, their results point to brain rhythms,
473 especially alpha, beta and gamma, as potential markers of flow state arising in tasks requiring
474 highly specialization such as playing a musical instrument (Farrugia et al., 2021), writing a
475 scientific manuscript (Moreno et al., 2020) or crossing a 15-metre-high tightrope (Leroy &
476 Cheron, 2020). Interestingly, these studies suggest the use of peripheral psychophysiological
477 measures (e.g., electrocardiogram or galvanic skin conductance) as complementary measures
478 that may help identify and characterize flow state (see Peifer and Tan, 2021, for a review).
479 However, the case studies included in this review are exposed to a moderate risk of bias, which
480 further limits the drawing of conclusions (see Risk of bias, in Supplementary material).

481 *Team flow*

482 Although most flow research has focused on individual participants, in recent years, there has
483 been a growing interest in the so-called team flow phenomenon (i.e., group flow, collective
484 flow), due to its potential applications in business and sports teams or artistic groups (Pels et
485 al., 2018). Team flow is conceptualized by van den Hout and collaborators (2018) as a state of
486 flow shared by a small group that results from a dynamic and optimal interaction between
487 people while executing interdependent individual tasks. Very recently, Shehata and
488 collaborators (2021) attempted to identify the EEG correlates of this collective flow experience.
489 In their study, 10 pairs of participants matched on the basis of their game skills and musical
490 tastes played a music rhythm game. Flow level was manipulated by scrambling the music of
491 the game (i.e., a reversed and shuffled version of the music was played, modifying the intrinsic
492 enjoyment dimension of flow, instead of the skill-difficulty balance) and by whether
493 participants could see or not their partner. As a result, participants simulated playing an
494 instrument in 3 different experimental conditions (i.e., team flow, flow only and team only)
495 while their brain activity was recorded with EEG. Interestingly, they validated their
496 experimental manipulation with subjective ratings of the flow state and objective measures of

497 task-irrelevant auditory-evoked potentials—in line with the dual-task paradigms hypothesis
498 above, e.g., Núñez-Castellar et al. (2019)—. The results of Shehata and collaborators (2021)
499 pointed to higher beta and gamma power in the middle temporal cortex (MTC) and enhanced
500 neural synchrony as correlates of team flow. Furthermore, they found lower beta and gamma
501 power in the PFC in the flow conditions compared with the no-flow conditions, which is
502 consistent with previous observations with fMRI (Ulrich et al, 2016a, 2016b, 2014).

503 Taken together, the evidence from EEG studies suggest that flow state might be linked
504 to changes in specific brain rhythms (i.e., theta, alpha, beta and gamma). However, the
505 experimental designs and paradigms implemented in these studies do not allow to elucidate
506 whether these changes in brain activity can be considered a consequence of experiencing flow
507 or a mere neural correlate of a closely related state (e.g., full attention), which does not
508 necessarily imply to be in flow.

509

510 **3.4. Research on brain stimulation: tDCS**

511 Throughout the literature on the neural basis of the flow state only two studies have
512 used tDCS to facilitate the emergence of flow state and explore its neural correlates (Gold &
513 Ciorciari, 2019; Ulrich et al., 2018). Both studies represent an innovative approach, in an
514 attempt to establish causal rather than correlational relationships. These studies tried to induce
515 flow state in healthy participants by increasing or decreasing the excitability of regions of the
516 cerebral cortex that would be involved in flow, according to the scarce existing literature (e.g.,
517 Ulrich et al., 2016a, 2016b, 2014). In a first study, Ulrich and collaborators (2018) recruited 22
518 participants to perform an arithmetic task with three difficulty conditions (i.e., low, adjusted,
519 high) while applying tDCS in combination with perfusion MRI. Participants performed the task
520 in three separate experimental sessions under anodal, cathodal or sham stimulation at Fpz, an
521 electrode location associated with the MPFC. Contrary to what they expected, the subjective
522 experience of flow was similar across the different tDCS conditions. However, in a further
523 exploratory analysis, participants were divided into two subgroups (i.e., high-flow and low-
524 flow) according to the median split of the flow index obtained in the sham condition. When
525 brain activity of both groups was compared, they observed that the low-flow group showed
526 higher deactivation of the right amygdala associated with an increase in the flow index
527 compared to the high-flow group. The authors concluded that individuals less susceptible to

528 flow state may benefit more than high-flow individuals from active tDCS in the MPFC.
529 However, due to the post-hoc exploratory nature of these analyses, and the fact that Ulrich and
530 collaborators (2018) found no differences in the reported flow state between the sham, anodal
531 and cathodal stimulation conditions, no conclusions about the role of the MPFC can be drawn
532 from these results.

533 Gold and Ciorciari (2019) investigated whether increased excitability in the right
534 parietal cortex and decreased excitability in the left DLPFC (anodal tDCS at P6 and cathodal
535 at F3) would result in greater flow experience, as measured by the Flow State Scale (Jackson
536 & Marsh, 1996). To do so, they conducted two experiments: one with expert video game
537 players (n = 11), and another one with non-experts (n = 21). Both groups played Tetris at three
538 difficulty levels (i.e., low, adaptive, and high). Researchers found that both groups (regular
539 gamers and non-gamers) reported higher scores of flow experience after the tDCS stimulation
540 compared with the sham condition. According to previous research, anodal parietal stimulation
541 appears to increase connectivity within neural networks, including inferior and superior parietal
542 along with the cerebellum, which has been linked to learning outcomes (Hunter et al., 2015).
543 On the other hand, DLPFC inhibition seems to enhance dynamic balance between explicit and
544 implicit systems (Eichenbaum & Cohen, 2004). In this line, the authors suggest that increased
545 right parietal activity together with decreased activity in the left DLPFC may foster flow
546 experience.

547 To sum up, while tDCS studies could help clarify some of the contradictions found in
548 the literature on the neural basis of flow state, the paucity of research to date (only two studies
549 so far) does not allow drawing any definitive conclusion about the involvement of specific
550 areas in flow state. In addition, it is important to highlight that tDCS has courted significant
551 controversy in the last years due to failed replication attempts, unknown physiological basis,
552 and variability in outcomes, resulting in skepticism regarding its reported effects (e.g., Filmer
553 et al., 2020; Parkin et al., 2019).

554

555 **4. Discussion**

556 The purpose of the present study was to systematically review the existent empirical
557 evidence on the neural correlates of flow state. We found a total of 25 studies using a wide
558 range of strategies to experimentally address flow state and its neural dynamics and revised

559 them from a critical perspective, an approach that had not been pursued before in the literature
560 on the potential neural mechanisms of flow. After scrutinizing the experimental paradigms
561 implemented and their resulting findings, it is concluded that the extant evidence is sparse and
562 inconclusive, with major methodological shortcomings that prevent us from drawing solid
563 conclusions about the neural correlates of flow state. Nevertheless, these investigations were
564 pioneering in the study of flow state from a neuroscientific perspective and their findings help
565 speculate about the potential neural correlates of flow that future studies may confirm.

566 In general, the studies using neuroimaging techniques while (trying to) inducing flow
567 seem to converge on the key role of structures linked to attention, executive function and
568 reward systems, giving to the anterior brain areas (e.g., the DLPC) a crucial role in the
569 experience of flow. However, the dynamics of these brain regions during flow state are
570 inconsistent across studies. Studies using fMRI report mixed patterns of activation and
571 deactivation of specific frontal areas such as the IFG and the medial prefrontal cortex (Ulrich
572 et al., 2014, 2016a, 2018), the DLPC (Huskey, Craighead, et al., 2018; Huskey, Wilcox, et al.,
573 2018) or the default mode network (Ju & Wallraven, 2019). In a similar vein, findings from
574 fNIRS studies are especially inconsistent, showing increased (de Sampaio Barros et al., 2018;
575 Yoshida et al., 2014) and decreased prefrontal activity (Hirao, 2014) during flow state, as well
576 as no significant prefrontal activity changes (Harmat et al., 2015). Regarding brain oscillatory
577 activity, EEG studies point to increased power of particular brain rhythms such as theta
578 (Katahira et al., 2018; Knierim et al., 2018) and alpha (Knierim et al., 2018; Núñez Castellar
579 et al., 2019) at frontal locations during flow state. Finally, tDCS studies also suggest a central
580 role of the prefrontal cortex in flow state although their results are mixed (Gold & Ciorciari,
581 2019; Ulrich et al., 2018).

582 Notably, the absence of consistent overlaps between the brain regions activated during
583 (presumably) flow states in the few studies included in the present systematic review is not
584 surprising. On the one hand, extremely different methodological approaches have been used to
585 induce flow, especially with regard to experimental tasks, including: arithmetic tasks, video
586 games, a verbal fluency test, writing a PhD thesis, a mental imagery task, running a marathon
587 or playing an instrument, among others. On the other hand, flow is a complex state which is
588 made up of different subcomponents —as indicated in the Introduction of this review,
589 according to the author of the original Theory of Flow, there are 9 different subcomponents of
590 flow state (Csikszentmihalyi, 1975)—. As mentioned above (see Results), some approaches

591 have focused on manipulating only one of these subcomponents of flow (e.g., skill-difficulty
592 balance, intrinsic reward). Therefore, studies that have induced different aspects of the flow
593 state can be expected to lead to different outcomes. These two major weaknesses in the existing
594 literature on the neural basis of flow make it particularly difficult to cluster studies, compare
595 their results, and above all, to draw firm conclusions.

596 As noted in the Introduction of this article, the two theoretical models (i.e., THH and
597 STF) that would account for the results summarized above stand for radically different
598 positions on the neural dynamics associated with the state of flow. On one hand, the THH
599 argues for a suppression of frontal activity during flow state which would reduce interference
600 of the explicit processing (e.g., self-referential thought) and facilitate implicit processing (i.e.,
601 automatized processes). Several studies reviewed here seem to provide partial support for this
602 theory (Gold & Ciorciari, 2019; Hirao, 2014; Katahira et al., 2018; Núñez Castellar et al., 2019;
603 Ulrich et al., 2014, 2016a, 2016b, 2018; Wollseiffen et al., 2016; Yun et al., 2017). However,
604 even assuming these studies were actually capturing the neural signatures of flow state, their
605 findings would suggest specific brain patterns associated with flow rather than a general
606 deactivation of frontal areas. On the other hand, the STF, based on findings from neuroimaging
607 studies on flow-like activities (e.g., hypnosis and meditation) showing strong brain frontal
608 activity (e.g., Newberg and Iversen, 2003), advocates for increased neural synchronization
609 between neural attention networks (i.e., executive, alerting and orienting) during flow state.
610 This principle of energetically-efficient brain functioning is a tentative (and highly speculative)
611 account to explain why flow is perceived as neither physically nor mentally depleting and
612 effortless despite the fact that the tasks commonly used to induce flow require a moderate-to-
613 high level of difficulty (Huskey, Craighead, et al., 2018; Huskey, Wilcox, et al., 2018). While
614 the STF seems to be supported by the results reported by several studies reviewed here (de
615 Sampaio Barros et al., 2018; Huskey, Craighead, et al., 2018; Huskey, Wilcox, et al., 2018;
616 Katahira et al., 2018; Klasen et al., 2012; Wolf et al., 2015; Yun et al., 2017), the
617 methodological limitations of these studies together with findings from some accounts that
618 seem to contradict this model (e.g., Huskey et al., 2018b, 2018a) cast doubts on it.

619 The Internal Model of Flow proposed by Gold and Ciorciari (2021) attempts to
620 reconcile these two seemingly contrary theories to explain most of the mixed evidence to date,
621 relying on the role of cerebellar regions. This model would be supported, for instance, by the
622 findings reported in Ulrich et al. (2016a), who observed activity in the cerebellum, premotor

623 regions and pre-supplementary motor cortex during flow state. Also compatible with the model
624 are the observations made by Klasen et al. (2012), who found activity in the cerebellum and
625 some regions of the reward system (e.g., putamen).

626 In any case, as already pointed out, despite the fact these studies are paving the road to
627 unveil the brain mechanisms supporting the flow experience, the evidence to date is sparse,
628 unreliable and inconclusive to allow any proper theoretical debate.

629

630 *The triad of (erroneous) inferences when studying flow*

631 Whatever the theoretical interpretation of the results reviewed here, one should have in
632 mind that a main part of this literature relies on three crucial inferences that, in our opinion,
633 limit the validity of their findings.

634 *Inference 1: Flow state arises in situations where the task's difficulty matches the skills of the*
635 *individual.* It is well-known that skills-difficulty balance is a necessary condition for flow state
636 to arise, but not sufficient since it represents only one feature of the experience of flow. For the
637 flow state to emerge, a task must also be regarded by the individual as critical and challenging
638 (but attainable), with immediate feedback about performance, carried out in a well-known task-
639 related scenario and during prolonged periods of time without interruption (Nakamura &
640 Csikszentmihalyi, 2014). Further, even if all these facilitating conditions are met it is
641 conceivable that flow state will not arise (i.e., we often face tasks whose difficulty matches our
642 skills and we do not experience flow). Thus, it seems unreasonable to assume that flow state
643 may arise performing a non-critical unmotivating task (i.e., sums) in an unrelated scenario (e.g.,
644 fMRI scanner) with continuous interruptions.

645 *Inference 2: The observed changes in brain activity are due to flow state.* Even assuming these
646 difficulty-based paradigms actually lead to flow state, it cannot be concluded that the changes
647 in brain activity observed during the flow condition are due to an experience of flow rather
648 than to a difference in the level of task's difficulty across conditions. These paradigms often
649 compare brain activity patterns collected during a moderate difficulty condition adjusted to the
650 subject's skill level (i.e., flow condition), with a low (i.e., boredom condition) or a high
651 difficulty condition (i.e., overload condition). The observed changes (e.g., changes in the
652 activity of prefrontal areas; e.g., Hirao, 2014; Katahira et al., 2018; Ulrich et al., 2016a;

653 Wollseiffen et al., 2016) may therefore be simply due to a variation in the difficulty level, as
654 noted by Ulrich and collaborators (2014). In fact, task difficulty manipulation induces an effort-
655 based cost-benefit analysis which is computed by prefrontal areas (Egner, 2009; Rushworth et
656 al., 2004). Moreover, in a recent study, Mallat and collaborators (2020), who used the task
657 difficulty manipulation approach, found that the highest level of effort mobilisation occurred
658 at an intermediate level of task difficulty, compared to very low or very high difficulty levels
659 (i.e., effortful control is maximal for moderate levels of difficulty). Consequently, any variation
660 in prefrontal activity found in the balanced skill-difficulty condition compared to low and high
661 difficulty conditions can be attributed to effort variations and not to a flow state. The absence
662 of an appropriate control condition prevents attributing the observed brain dynamics to the state
663 of flow (see Future directions section for recommendations on this issue).

664 *Inference 3: If the brain area X is active, then the cognitive process Y is engaged.* The reversal
665 inference is one of the most prominent inferential strategies in cognitive neuroscience (Nathan
666 & Del Pinal, 2017; Poldrack, 2006), and the study of the neural basis of flow has not been
667 exempted from it. In this particular case, this inference arises when the observed changes in
668 brain regions or systems previously associated with flow-related cognitive processes are
669 directly considered as a sign of the presence of flow state. Given the multi-functionality of most
670 brain areas and neural systems, it seems unreasonable to assume that all the observed brain
671 activity changes found during flow state would be selective of it, rather than a concomitant
672 neural correlated of any other related process. A clear example of that inference in flow
673 research is the key role of the cerebellum put forward by the Internal Model of Flow (Gold &
674 Ciorciari, 2021). While some studies found increased activity in the cerebellum during flow
675 state (Klasen et al., 2012; Ulrich et al., 2016a), such direct association would be questioned
676 when considering recent accounts of the cerebellum's involvement in cognitive and emotional
677 processes, in the same way that it regulates sensorimotor and vestibular control (e.g.,
678 Schmahmann et al., 2019).

679 In sum, when delving into what flow state is and how its correlates (i.e., neural,
680 cognitive, and phenomenological) can be measured, one may ultimately consider whether we
681 are indeed ready to identify and quantify reliable neural correlates of the flow state. In the next
682 section, potential solutions to these three major flaws in flow state research are directly
683 addressed.

684

685 4.1. Future directions

686 As mentioned along these lines, due to the intrinsic characteristics of the flow state, one
687 might argue that it is unlikely that flow could be triggered in controlled laboratory conditions
688 where neural activity can be reliably recorded. However, several considerations regarding
689 experimental design and flow measurements may provide useful avenues for future studies in
690 flow research.

691 First, a paradigm shift is needed, from the traditional experimental paradigm for
692 inducing flow state through arithmetic tasks to more intrinsically motivating tasks such as video
693 games or physical exercise. Video games are particularly suitable for studying the flow state in
694 a laboratory because the scenario can be quite similar to a real situation, with low motor
695 activity, high levels of enjoyment and immersion. Moreover, the movement associated with
696 physical exercise and the need to be carried in ecological settings makes it more complicated
697 to collect quality data on electrical activity (e.g., portable EEG systems can be used, but not
698 high-density EEG or other types of neuroimaging techniques), a constraint that is not present
699 when video games are used as an experimental task. In addition, video games are often played
700 over extended periods of time, facilitating and increasing the likelihood of flow.

701 Second, there is a need for studies with large samples of experts since they are more
702 likely to experience prolonged states of flow, as well as studies in which individuals are trained
703 in particular activities to experience flow state more easily. Notably, larger sample sizes in
704 general are necessary—more than half of the studies included in the present review have
705 samples of less than 20 participants—, so that studies attempting to observe the neural
706 correlates of flow have sufficient statistical power to detect the effect, if present. In this sense,
707 the number of video game players is growing every year and would facilitate the collection of
708 large sample sizes of experts, which again points to video games as a promising activity to
709 experimentally address flow state under controlled conditions.

710 Third, implementing repeated measures designs, with several experimental sessions in
711 different days with the same subjects, would not only increase the chances of each subject to
712 experiencing flow, but would also enhance the individual's familiarity with the situation,
713 presumably fostering the emergence of flow. Moreover, it would provide a more appropriate
714 control condition for flow experiments. That is, by having brain recordings of each individual
715 during different sessions (or periods during the same session) with similar task conditions (e.g.,

716 in terms of difficulty), one may compare brain activity patterns in periods when the individual
717 experienced the flow state with those when they did not.

718 Fourth, the use of methodologies that allow ongoing tracking of the subjective
719 experience of flow state without continuous interruptions, so that the transient fluctuations of
720 the subject's state throughout the task can be captured. Recently, a novel phenomenological
721 method has been developed for capturing continuous subjective experiences: Temporal
722 experience tracing (Jachs, 2021). This method requires participants to retrospectively graph the
723 intensity of an experience along a particular phenomenological dimension (e.g., flow, attention,
724 boredom) over time. This would reduce the number of interruptions during the task (asking for
725 self-reporting of several flow-related items), facilitating the occurrence and maintenance of
726 flow state. Furthermore, it would allow a fine-grained characterization of flow state temporal
727 fluctuations.

728 Fifth, the use of portable systems to measure brain activity (e.g., wearable Dry-EEG
729 headset) may help collect neural data in ecological situations where it is easier to trigger an
730 experience of flow. In fact, in one of the most recent studies included in the review, Knierim
731 and collaborators (Knierim et al., 2021) employed an interesting portable EEG device, a 3D
732 printed Brain-Computer-Interface platform with c-shaped EEG electrode array, which, if
733 validated with a larger experimental sample, could be a promising tool for research on flow
734 states in facilitating contexts.

735 Sixth, something intriguing we found in the literature of flow state is the unjustified
736 misrepresentation of women. From the 25 studies included in this systematic review, only 14
737 included female participants (72.6% of the total sample were men). Some of them even justify
738 the selective inclusion of men to reduce putative sex differences due to hormonal alterations
739 during the menstrual cycle (Ulrich et al., 2014, 2018). However, the hormone-brain-cognition
740 relationship is not as straightforward as one might think (Fine, 2010, 2017; Weigard et al.,
741 2021), and brain differences between males and females appear trivial and population-specific
742 based on recent accounts (Eliot et al., 2021; Rippon, 2019). In any case, to be representative of
743 the whole population, studies should include male and female participants. We therefore
744 encourage researchers to design gender-balanced studies in the future to reduce this gap in flow
745 literature.

746 And last, but not least, future studies on the neural correlates of the flow state should
747 avoid falling into the erroneous inferences that have weakened the existing literature so far.
748 The use of tasks, procedures and contexts that facilitate the emergence of the flow state, such
749 as those stated above, must be accompanied by direct subjective (e.g., questionnaires) and
750 objective, albeit indirect (e.g., auditory evoked potentials), measures of the flow state.
751 Moreover, these measures should be implemented together with sophisticated control measures
752 of other variables that may be influencing changes in brain activity —e.g., effortful control (see
753 Inference 2 above), which could be controlled by measuring pre-ejection period (PEP) with
754 electrocardiogram (EKG), a reliable and valid index of mental effort mobilization (Mallat et
755 al., 2020)—. This will allow stronger links to be established between the recorded brain activity
756 and the flow state. Furthermore, the use of reverse inference (i.e., proposing which cognitive
757 processes may be involved in the flow state based solely on observed activity in specific areas)
758 should be avoided.

759

760 **4.2. Limitations**

761 The present systematic review is undermined by the small number of studies addressing
762 this topic. Only 25 studies were included, which were based on a wide range of paradigms and
763 analytical approaches. This small number of studies, together with the high heterogeneity
764 across them and the moderate risk of bias estimated for many of them (see Risk of bias, in
765 Supplementary material), drastically ruled out the possibilities of using meta-analytic
766 techniques since its potential results would be meaningless. Moreover, most of these studies
767 present important methodological limitations that considerably hamper the scope of our
768 conclusions.

769 The main objectives and methods (i.e., search protocol) were not pre-registered before
770 the systematic review was carried out, a practice that would have contributed to greater
771 transparency and avoidance of bias (Stewart et al., 2012), as well as the avoidance of possible
772 unintentional duplication of effort to collect neural correlates of the flow state. The reason why
773 this review was not pre-registered is that it was initially carried out as the first author's (CA)
774 final undergraduate project, under the supervision of LC and DS. Given the quality of that first
775 manuscript and the relevance of the topic, the authors decided to submit it to a peer-review

776 journal, after updating the list of papers with a second search (performed both by CA and LC)
777 and further rounds of amendments.

778

779 **4.3. Final conclusion**

780 The present systematic review synthesises and critically assesses the extant scientific
781 evidence on the neural correlates of flow state, questioning for the first time in the literature
782 the validity and reliability of the findings reported in the experiments attempting to capture the
783 brain signatures of flow experience. In general, studies addressing this topic are scarce,
784 showing large heterogeneity in the methods and inconsistency in the outcomes, which limits
785 any theoretical debate or potential application. Despite the absence of conclusive evidence, it
786 is important to note that these studies pave the way for future work and help speculate about
787 the potential neural signatures of flow state to drive future research on this topic.

788

789 **5. Acknowledgments**

790 This manuscript is dedicated to the memory of Professor Mihály Csíkszentmihályi
791 (1934-2021), whose pioneering work on flow state inspired countless ideas during the course
792 of this project and will undoubtedly continue inspiring future generations of flow researchers.

793

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Table 1
Characteristic of the studies investigating neural correlates of flow state

Study	N (f)	Age (SD/range)	Sample	Task	Flow measures	Main findings
fMRI						
Ulrich et al., 2014	27	23 ± 2.3	University students	Arithmetic task	Flow Index (9 Likert-scale items)	Increased activity in the left IFG, putamen and posterior cortical regions, and decreased activity in the MPFC, the left AMY, hippocampus and parahippocampal gyrus in the flow condition.
Ulrich, Keller & Grön, 2016a	23	24 ± 2.7	University students	Arithmetic task	SFPQ Flow Index	Increased activity in the IFG, left putamen and posterior cortical regions, and decreased activity in the MPFC, PCC and AMY in the flow condition.
Ulrich, Keller & Grön, 2016b	23	24 ± 2.7	University students	Arithmetic task	SFPQ Flow Index	Stronger down-regulatory influence of the DRN on the MPFC when participants experienced flow.
Huskey, Craighead, Miller & Weber, 2018	18 (14)	22.8	University students	P: video game S: visual RT task	Autotelic personality subscale of the AES	Increased activity in DLPFC, superior parietal lobe, precentral gyrus, dorsal anterior insula and putamen in the flow condition.
Huskey, Wilcox & Weber, 2018	18 (14)	22.8	University students	P: video game S: visual RT task	Autotelic personality subscale of the AES	Lower energetic cost in the flow condition. No greater connectivity between cognitive control and reward networks in the flow condition.
Klasen et al., 2012	13	23	Regular video gamers	Video game	-	Increased activity in sensorimotor networks and the cerebellum during game moments with higher probability of flow state.
Ju & Wallraven, 2019	31	24.8 ± 3.6	Regular video gamers	Video game	GEQ	Correlation between flow and the activity of regions related to visual and spatial processing and attentional processes. Negative correlation with the activity of the DMN.
fNIRS						
Yoshida et al., 2014	15 (9)	22.0 ± 1	University students	Video game	Flow state scale for occupational tasks	Increased activity in VLPFC, FPA, and DLPFC during flow condition.
Harmat et al., 2015	35 ^a	27.8 ± 5.4	University students	Video game	FSS-2	No association between frontal cortical oxygenation and flow scores.
Hirao, 2014	60 (22)	19.5 ± 0.9	University students	Verbal fluency test	Flow Questionnaire	Negative correlation between the average oxygenated hemoglobin in the prefrontal cortex and flow scores.

de Sampaio Barros, 2018	20 (7)	26.4 ± 4.8	Adult volunteers	Video game	Flow Short Scale	Flow condition correlated with higher concentration of oxygenated hemoglobin in regions of the frontoparietal network.
Yu et al., 2022	40 (18)	19-26	University students	Video game	Flow Short Scale	Flow level correlated linearly with the increase in oxygenated hemoglobin concentration level in DLPFC and FPA.

EEG

Katahira et al., 2018	16 (6)	21.9 ± 1.1	University students	Arithmetic task	Flow index	Correlation between flow and theta activity in frontal electrodes, and alpha activity in fronto-central electrodes.
Knierim et al., 2018	7	21-30	University students	Writing PhD thesis Arithmetic task	Flow Short Scale	Increased theta and alpha activity in frontal electrodes as task difficulty increases.
Knierim et al., 2021	6	24-30	University students	Arithmetic task	Flow Short Scale	Increased alpha temporal activity in the flow condition.
Nuñez-Castellar et al., 2019	18 (9)	28.5 ± 4.6	Casual video gamers	P: video game S: auditory oddball	Flow Short Scale Flow Questionnaire	Lower amplitude of P300 in the flow condition and increased frontal alpha in the flow condition.
Yun et al., 2017	29 (5)	23.5 ± 3.4	Regular video gamers	P: video game S: random sounds	Reported flow level (Think Aloud design)	Lower increase of beta band power evoked by the random sounds in the ACC during flow compared to non-flow state.
Wolf et al., 2015	29 (9)	23.3	Amateur and expert table tennis players	Mental motor imagery	Flow Short Scale	Flow correlates with less temporal activity in the left hemisphere and increased activity in right temporal hemisphere in the expert group.
Wollseiffen et al., 2016	11 (5)	36.5 ± 7	Ultramarathon runners	P: 6h-running S: Arithmetic task	FSS-2 short version FSS-2 long version	Decreased frontal beta activity and increased flow after the first hour. No correlation between flow state and beta or alpha after the first hour.
Farrugia et al., 2021	1	53	Musician	Improvisation	Concentration STR	Positive correlation between fast perceived passage of time and brain rhythms (theta and beta) activity.
Moreno et al., 2019	2 (1)	-	Regular video gamer Academic writer	Video game Scientific article	FSS	Increased beta and gamma activity during flow condition in both participants.
Leroy & Chéron, 2020	1	-	Tightrope walker	Crossing a tightrope	Flow Short Scale	Increased alpha activity during the flow period.
Shehata et al., 2021	15 (10)	18-35	-	Video game	Flow Index (6 Likert-scale items)	Higher beta and gamma power in MTC during team flow condition.

tDCS

Ulrich et al., 2018	22	24.9 ± 2.2	University students	Arithmetic task	Flow Index SFPQ	No effects of TDCS in the MPFC in subjective experience of flow.
Gold & Ciorciari, 2019	E1: 11 E2: 21 (11)	E1: 2 ± 7.1 E2: 30.9	E1: regular video gamers E2: non-gamers	Video games	FSS	Decreased DLPFC activity and increased right parietal cortex activity associated with flow state in regular video gamers and non-gamers.

SD, standard deviation; fMRI, functional magnetic resonance imaging; f, female; IFG, inferior frontal gyrus; MPFC, medial prefrontal cortex; P: primary task (dual task paradigm); S: secondary task (dual task paradigm); AMY, amygdala; SFPQ, Swedish Flow Proneness Questionnaire; GEQ, Gaming Experience Questionnaire; DMN, Default Mode Network; PCC, posterior cingulate cortex; FSS-2, Event Experience Scale (2); DRN, dorsal raphe nucleus; DLPFC, dorsolateral prefrontal cortex; AES, Activity Experience Scale; RT, reaction time; VLPFC, ventrolateral prefrontal cortex; FPA, frontal pole area; fNIRS, functional near-infrared spectroscopy; EEG, electroencephalography; STR, Subjective Temporal Resolution; FSS, Flow State Scale; MTC, middle temporal cortex; TDCS, transcranial direct current stimulation; E1, experiment number 1; E2, experiment number 2.

^a Sex is not specified

Supplementary material

The brain in flow: a systematic review on the neural basis of the flow state

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1. EXCLUDED STUDIES

Excluded studies for not meeting the inclusion criteria (k = 24):

No peer review:

Bishop, A., MacNeil, E., & Izzetoglu, K. (2021, July). Cognitive Workload Quantified by Physiological Sensors in Realistic Immersive Settings. In *International Conference on Human-Computer Interaction* (pp. 119-133). Springer, Cham.

Bombeke, K., Dongen, A. V., Durnez, W., Anzolin, A., Almgren, H., All, A., ... & Núñez Castellar, E. P. (2018, July). Do not disturb: psychophysiological correlates of boredom, flow and frustration during VR gaming. In *International Conference on Augmented Cognition* (pp. 101-119). Springer, Cham.

Burns, A., & Tulip, J. (2017, August). Detecting flow in games using facial expressions. In *2017 IEEE Conference on Computational Intelligence and Games (CIG)* (pp. 45-52). IEEE.

Carofiglio, V., De Carolis, B. N., & D'Errico, F. (2019, September). A BCI-based Assessment of a Player's State of Mind for Game Adaptation. In *GHITALY@ CHIItaly*.

Cassani, R., Tiwari, A., Posner, I., Afonso, B., & Falk, T. H. (2020, October). Initial investigation into neurophysiological correlates of argentine tango flow states: a case study. In *2020 IEEE International Conference on Systems, Man, and Cybernetics (SMC)* (pp. 3478-3483).

Gupta, K., Zhang, Y., Pai, Y. S., & Billinghamurst, M. (2021). VR-Wizard: Towards an Emotion-Adaptive Experience in VR. In *SIGGRAPH Asia 2021 Posters* (pp. 1-2).

Knierim, M. T., Nadj, M., & Weinhardt, C. (2019). Flow and Optimal Difficulty in the Portable EEG: On the Potentiality of using Personalized Frequency Ranges for State Detection. In *CHIRA* (pp. 183-190).

Labonté-Lemoyne, É., Léger, P. M., Resseguier, B., Bastarache-Roberge, M. C., Fredette, M., Sénécal, S., & Courtemanche, F. (2016, May). Are we in flow neurophysiological correlates of flow states in a collaborative game. In *Proceedings of the 2016 CHI*

Conference Extended Abstracts on Human Factors in Computing Systems (pp. 1980-1988).

Li, M., Chen, C., Hua, C., & Guan, X. (2019, May). CFlow: A learning-based compressive flow statistics collection scheme for SDNs. In *ICC 2019-2019 IEEE International Conference on Communications (ICC)* (pp. 1-6). IEEE.

Mann, S., Defaz, D., Abdulazim, T., Lam, D., Alford, M., Stairs, J., & Mann, C. (2019, June). Encephalogram TM (brain/mind games): inclusive health and wellbeing for people of all abilities. In *2019 IEEE Games, Entertainment, Media Conference (GEM)* (pp. 1-10). IEEE.

Plotnikov, A., Stakheika, N., De Gloria, A., Schatten, C., Bellotti, F., Berta, R., ... & Ansovini, F. (2012, July). Exploiting real-time EEG analysis for assessing flow in games. In *2012 IEEE 12th International Conference on Advanced Learning Technologies* (pp. 688-689). IEEE.

Sinha, A., Gavvas, R., Chatterjee, D., Das, R., & Sinharay, A. (2015, October). Dynamic assessment of learners' mental state for an improved learning experience. In *2015 IEEE frontiers in education conference (FIE)* (pp. 1-9). IEEE.

Wang, C. C., & Hsu, M. C. (2013). Flow experience and challenge-skill balance in e-learning. In *2013 Pacific Asia Conference on Information Systems (PACIS)*.

No specific measures of flow state (e.g., measures of creativity, performance, attention, or customer experience):

Budnik-Przybylska, D., Kastrau, A., Jasik, P., Kaźmierczak, M., Doliński, Ł., Syty, P., & Bertollo, M. (2021). Neural oscillation during mental imagery in sport: an olympic sailor case study. *Frontiers in Human Neuroscience*, 15.

Kwon, S. H., Lee, Y. J., & Kwon, Y. J. (2020). Why do students fall into webtoon viewing while they give up mathematics? - An fMRI study. *International Journal of Knowledge and Learning*, 13(3), 201-213.

McMahan, T., Parberry, I., & Parsons, T. D. (2015). Evaluating player task engagement and arousal using electroencephalography. *Procedia Manufacturing*, 3, 2303-2310.

Rothlein, D., DeGutis, J., & Esterman, M. (2018). Attentional fluctuations influence the neural fidelity and connectivity of stimulus representations. *Journal of cognitive neuroscience*, 30(9), 1209-1228.

Škola, F., Rizvić, S., Cozza, M., Barbieri, L., Bruno, F., Skarlatos, D., & Liarokapis, F. (2020). Virtual reality with 360-video storytelling in cultural heritage: Study of presence, engagement, and immersion. *Sensors*, 20(20), 5851.

Wang, C. C., & Hsu, M. C. (2014). An exploratory study using inexpensive electroencephalography (EEG) to understand flow experience in computer-based instruction. *Information & Management*, 51(7), 912-923.

Weber, R., Alicea, B., Huskey, R., & Mathiak, K. (2018). Network dynamics of attention during a naturalistic behavioral paradigm. *Frontiers in human neuroscience*, 12, 182.

No specific measures of brain activity during flow state (i.e., correlations between flow state and brain activity are not analyzed):

Wang, Z., Li, M., & Yuan, J (2022). An Empirical Study of Geography Learning on Students' Emotions and Motivation in Immersive Virtual Reality. In *Frontiers in Education* (p. 74). Frontiers.


Wu, S. F., Lu, Y. L., & Lien, C. J. (2021). Detecting students' flow states and their construct through electroencephalogram: Reflective flow experiences, balance of challenge and skill, and sense of control. *Journal of Educational Computing Research*, 58(8), 1515-1540.

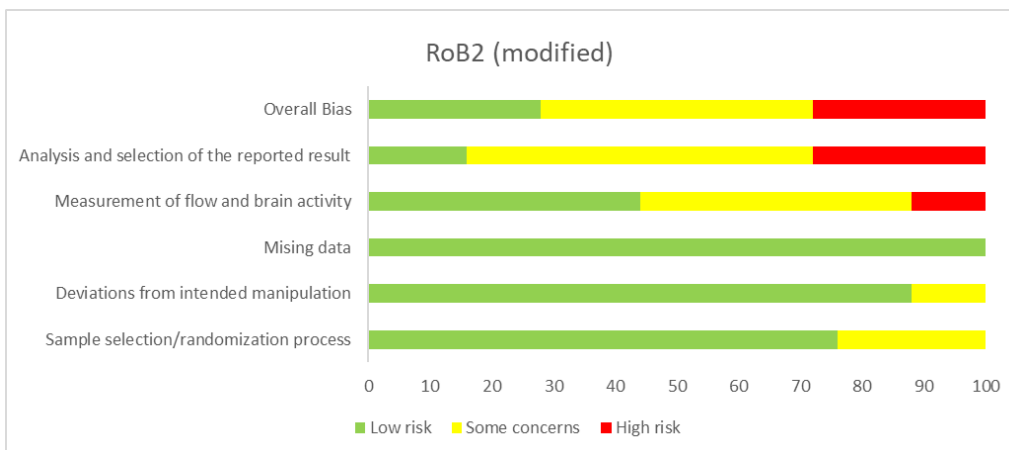
Wu, S. F., Lu, Y. L., & Lien, C. J. (2021). Measuring effects of technological interactivity levels on flow with electroencephalogram. *IEEE Access*, 9, 85813-85822.

Yang, X., Lin, L., Cheng, P. Y., Yang, X., & Ren, Y. (2019). Which EEG feedback works better for creativity performance in immersive virtual reality: The reminder or encouraging feedback?. *Computers in Human Behavior*, 99, 345-351.

2. RISK OF BIAS

Table summarizing risk of bias assessment of the 25 selected studies with a slightly modified version of the RoB 2 tool (revised Cochrane risk of bias tool for randomised trials):

References	D1	D2	D3	D4	D5		
Ulrich et al., 2014	+	+	+	!	-	-	
Ulrich, Keller & Grön, 2016a	+	+	+	+	-	-	
Ulrich, Keller & Grön, 2016b	+	+	+	+	!	!	
Huskey, Craighead, Miller & Weber, 2018	+	+	+	!	!	!	
Huskey, Wilcox & Weber, 2018	+	+	+	!	!	!	D1 Sample selection/randomization process
Klasen et al., 2012	+	+	+	-	+	-	D2 Deviations from the intended manipulation
Ju & Wallraven, 2019	+	+	+	+	!	!	D3 Missing data
Yoshida et al., 2014	+	+	+	+	!	!	D4 Measurement of flow and brain activity
Harmat et al., 2015	!	+	+	+	!	+	D5 Analysis/selection of the reported result
Hirao, 2014	!	+	+	-	-	-	
de Sampaio Barros, 2018	+	+	+	!	-	-	
Yu et al., 2022	+	+	+	+	!	!	
Katahira et al., 2018	+	+	+	+	!	+	
Knierim et al., 2018	+	+	+	!	-	-	
Shehata et al., 2021	+	+	+	!	+	+	
Nuñez-Castellar et al., 2017	+	+	+	+	+	+	
Yun et al., 2017	+	+	+	!	!	!	
Knierim et al., 2021	+	+	+	!	!	!	
Wolf et al., 2015	!	+	+	!	!	!	
Wollseiffen et al., 2016	+	+	+	+	!	+	
Farrugia et al., 2021	!	!	+	!	-	!	
Moreno et al., 2019	!	!	+	-	-	-	
Leroy & Chéron, 2020	!	!	+	+	+	+	
Ulrich et al., 2018	+	+	+	!	!	!	
Gold & Ciorciari, 2019	+	+	+	+	!	+	



3. FUNDING SOURCES

Table summarizing the funding sources of the 25 selected articles:

All authors in the 25 studies declare that they have no conflict of interest.

Study	Funding sources
Ulrich et al., 2014	German Research Foundation (DFG) to Johannes Keller [grant number KE 913/5-1]
Ulrich, Keller & Grön, 2016a	German Research Foundation (DFG) to Johannes Keller [grant number KE 913/5-1]
Ulrich, Keller & Grön, 2016b	German Research Foundation (DFG) to JK [grant number KE 913/5-1]
Huskey, Craighead, Miller & Weber, 2018	-. ^a
Huskey, Wilcox & Weber, 2018	The University of California Santa Barbara George D. McCune Dissertation Fellowship (to R. H.), University of California Santa Barbara Brain Imaging Center, the University of California Santa Barbara Academic Senate (grant AS-8-588817-19941-7 to R. W.), and the Institute for Social, Behavioral and Economic Research (grant ISBG-SS17WR-8-447631-19941 to R. W.)
Klasen et al., 2012	German Research Foundation (Deutsche Forschungsgemeinschaft (DFG), IRTG 1328; & MA 2631-4) and the IZKF Aachen (N2-3)
Ju & Wallraven, 2019	Basic Science Research Program through the National Research Foundation of Korea funded by the Ministry of Science, ICT & Future planning (NRF-2015S1A5A8018 , NRF-2017M3C7A1041817) and the Brain Korea 21plus program through the National Research Foundation of Korea (NRF) funded by the Ministry of Education
Yoshida et al., 2014	-. ^a
Harmat et al., 2015	Sven and Dagmar Salén Foundation, the Swedish Scientific Council (521-2010-3195), the Freemasons in Sweden Foundation for Children's Welfare, and the Bank of Sweden Tercentenary Foundation (M11-0451:1)
Hirao, 2014	-. ^a
de Sampaio Barros, 2018	Marcelo Felipe de Sampaio Barros was supported by a scholarship from the 820 Cogn Affect Behav Neurosci (2018) 18:810–823 CAPES Foundation of the Ministry of Education of Brazil, Brasília–DF 70040-020, Brazil (No. 99999.010663/2014-02). Rémi Radel was supported by a grant of the Agence Nationale de la Recherche (ANR–JCJC, 2013-069)

Yu et al., 2022	Social Science Planning Fund Program of Shandong [grant number: 18CCXJ23]
Katahira et al., 2018	Japan Society for the Promotion of Science (Grant Number JP15H05347), MEXT-Supported Program for the Strategic Research Foundation at Private Universities, 2014–2018 (Grant Number S1411038) and Center of Innovation Program from Japan Science and Technology Agency, JST
Knierim et al., 2018	- ^a
Knierim et al., 2021	- ^a
Nuñez-Castellar et al., 2019	Postdoctoral grant from the Ghent University special research fund (DPO/AWS-AAP/PP01/KD/30267635) and short-stay mobility grant COST-Quality of Experience in Multimedia Systems and Services (QUALINET)
Yun et al., 2017	JST-ERATO, JST-CREST, Tamagawa-Caltech gCOE programs, Grant-in-Aid for Scientific Research (Kakenhi) in Japan, and Basic Science Research Program through the National Research Foundation of Korea (NRF) funded by the Ministry of Education, Science and Technology (2013R1A6A3A03020772)
Wolf et al., 2015	German research associations: the German research association, DFG, (BI 195/67-1 and Kosellek), the German Center for Diabetes Research (DZD, 01G/0925), the Eva and Horst Köhler Foundation and the VW Foundation.
Wollseiffen et al., 2016	- ^a
Farrugia et al., 2021	Britanny region, grant SAD-MultiGSP (Award ID: SAD-2019) and the Finistere department, grant MultiGSP
Moreno et al., 2019	- ^a
Leroy & Chéron, 2020	The Belgian National Fund for Scientific Research (FNRS), the Research Funds, the Leibniz Fund of the Université Libre de Bruxelles and the Université de Mons (Belgium), and the European Commission Project EACEA 34/2018-2019 ‘Wires Crossed – Head, Heart, Balance / WCHHB’
Shehata et al., 2021	The Program for Promoting the Enhancement of Research Universities funded to Toyohashi University of Technology and Grants-in-Aid for Scientific Research (Fostering Joint International Research (B), Grant Number 18KK0280) (M.S. and S.N.), Sponsored Research by Qneuro, Inc. (M.S. and S.S.), Translational Research Institute through NASA Cooperative Agreement NNX16AO69A (M.S. and S.S.), and Japan Science and Technology (JST)-CREST Grant JPMJCR14E4 (to S.S.). The University of Hong Kong Postgraduate Scholarship Program. The University of Hong Kong General Research Fund and the Cooperative Research Project Program of the Research Institute of Electrical Communication, Tohoku University. Australian Research Council Discovery Projects Grants DP180104128 and DP18010039, and Australian Government Research Training Program Scholarship
Ulrich et al., 2018	- ^a

Gold & Ciorciari, 2019

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