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Future Portrait of the Athletic Brain: Mechanistic Understanding of Human Sport Performance Via Animal Neurophysiology of Motor Behavior

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Sport performances are often showcases of skilled motor control. Efforts to understand the neural processes subserving such movements may teach us about general principles of behavior, similarly to how studies on neurological patients have guided early work in cognitive neuroscience. While investigations on non-human animal models offer valuable information on the neural dynamics of skilled motor control that is still difficult to obtain from humans, sport sciences have paid relatively little attention to these mechanisms. Similarly, knowledge emerging from the study of sport performance could inspire innovative experiments in animal neurophysiology, but the latter has been only partially applied. Here, we advocate that fostering interactions between these two seemingly distant fields, i.e., animal neurophysiology and sport sciences, may lead to mutual benefits. For instance, recording and manipulating the activity from neurons of behaving animals offer a unique viewpoint on the computations for motor control, with potentially untapped relevance for motor skills development in athletes. To stimulate such transdisciplinary dialog, in the present article, we also discuss steps for the reverse translation of sport sciences findings to animal models and the evaluation of comparability between animal models of a given sport and athletes. In the final section of the article, we envision that some approaches developed for animal neurophysiology could translate to sport sciences anytime soon (e.g., advanced tracking methods) or in the future (e.g., novel brain stimulation techniques) and could be used to monitor and manipulate motor skills, with implications for human performance extending well beyond sport.

Keywords: information processing, motor control, neural networks, animal models, sport performance

INTRODUCTION

Numerous sport performances appear esthetically appealing and deceptively simple. At the heart of such performances are complex dynamics involving body mechanics and neural control. Here we argue for a stronger interaction between sport neuroscience and non-human (henceforth simply animal or basic) neurophysiology, to provide mutual benefits for both disciplines, i.e., behavioral

115 outcome in sport and cellular mechanisms in animal
116 studies, toward a deeper understanding of the nature of
117 motor performance.

118 Indeed, many sports gestures can be regarded as prominent
119 showcases of skilled motor control and thus, considering the
120 central nervous system (CNS) as a machine producing adaptable
121 movements, are of great relevance for various disciplines
122 including cognitive neuroscience (Shadmehr and Krakauer,
123 2008; Graziano, 2009; Yarrow et al., 2009). Unsurprisingly,
124 investigations on the neural bases of sport performance
125 raised interest also in human physiology and biomedicine.
126 Classic physiological research focused, among others processes,
127 on fatigue, with the long-dominating view considering it a
128 muscular limit. This view is now partially disrupted in favor
129 of evidences indicating that, at the bottom of muscular fatigue,
130 there is also an exhaustion of the nervous system (Noakes,
131 2012). In biomedicine, sport was assessed mostly as either a
132 health-promoting or harming intervention. In the first case,
133 sport serves to model increased level of physical activity,
134 with a typical intervention goal being prevention of non-
135 neural pathologies associated with sedentary lifestyle, while
136 a more recent focus has been to use sport as a way of
137 promoting “brain health” (Boecker et al., 2012; Malm et al.,
138 2019; Logan et al., 2020). In the second case, sport entails
139 increased risks for traumatic CNS injuries (especially sports
140 like Boxing or American Football), and it is possible to predict
141 the magnitude of the behavioral impairments based on the
142 intensity of the head impacts (Gavett et al., 2011; Castellani
143 and Perry, 2017; Mckee et al., 2018; Leeds et al., 2019). Also,
144 epidemiological data support the hypothesis that some athletes,
145 like football players, have an increased risk of developing certain
146 neurodegenerative diseases, including possibly amyotrophic
147 lateral sclerosis (Blecher et al., 2019).

148 A more recent research line aims to investigate the neural
149 bases of motor performance, and a first milestone has been
150 to uncover behavioral and neural differences between naive
151 and expert athletes, contributing to the establishment of sport
152 neuroscience (Yarrow et al., 2009; University of Tsukuba,
153 2019). This new field leverages mainly upon concepts and
154 methodologies of sport psychology and cognitive neuroscience
155 (Milne, 2007; Gee, 2010; Zhou and Zhou, 2019), and the
156 integration of methods and/or concepts emerging from
157 neurophysiological studies will likely provide a groundbreaking
158 stimulus toward a mechanistic understanding of the neural bases
159 of human performance.

162 ON THE DEFINITIONS OF SPORT

164 While in some contexts, physical activity and exercise (Caspersen
165 et al., 1985) are terms used interchangeably with the term
166 sport, for the latter we embrace the following definition: “an
167 activity involving physical exertion and skill, especially one
168 regulated by set rules or customs in which an individual or team
169 competes against another or others” (Oxford English Dictionary,
170 2020). Also, the effects of physical activity and exercise at
171 the neural level are already well established in human and

172 animal studies; sport has lagged behind. In addition, sport is
173 an umbrella term encompassing disparate disciplines associated
174 with quite heterogeneous sets of cognitive and motor abilities.
175 Broadly, two sport categories can be distinguished, namely,
176 closed skill sports (CSS) and open skills sports (OSS), whereby
177 the first category includes those sports that are often based
178 on the alternate and rhythmic repetition of limb movements,
179 where the context is relatively constant and predictable (e.g.,
180 swimming) (Wang et al., 2013a). At variance, in OSS the
181 athlete’s performance is embedded in an environment that
182 is dynamic, difficult to predict, and externally paced (e.g.,
183 tennis) (Wang et al., 2013a; Bove et al., 2017). Hence, while a
184 CSS also involves central networks associated to, e.g., energy
185 management, most CSSs are mainly based on variation of
186 locomotion parameters and thus could be regarded as “less
187 cognitive” and more associated with low-level motor control and
188 circuits (i.e., spinal) (Wang et al., 2013a). In OSS, on top of fine-
189 tuning of locomotion parameters, other aspects, such as skilled
190 object manipulation, action observation and anticipation, and a
191 coral, tactical strategy, are necessary to succeed. It may thus seem
192 intuitive to consider animal modeling of, e.g., running to be less
193 complex than, say, tennis and that differential insights on the
194 cognitive bases of sport performance may be extracted. Here, we
195 exclude sports involving the active involvement of animals (such
196 as horse racing).

197 In addition to canonical sports, competitive video gaming
198 (Winkie, 2019) is emerging as a new sport discipline termed
199 electronic sport (eSport). Movements of eSport athletes are
200 usually constrained to keystrokes, gamepads, joystick, and
201 mouse movements, which facilitates, compared to many real
202 world sports, hypothesis testing and task manipulations typical
203 of laboratory-based experimentation. Critically, virtual reality
204 studies are routinely performed in both humans and animals
205 and could be readily adapted to model eSport, which could
206 be harvested toward a mechanistic understanding of motor
207 performance (Sousa et al., 2020). Whether eSport can be
208 considered as a “true” sport is still debated (Parry, 2019); however,
209 it is worth mentioning that eSport-related activities are on the
210 verge of being incorporated in future Olympics (Grohmann,
211 2017). Independently of such organizations’ regulations, eSports
212 could be an important research tool for assessing cognitive
213 processes underlying some aspects of sport performance, similar
214 to what has been done using, e.g., flight simulations for military
215 training/testing. Future research will establish the extent to
216 which spatial scaling of the motor effector used in virtual
217 versus physical environments could influence the performance
218 and/or whether scale-invariant parameters [possibly obeying the
219 fractal ordering principle, (Turvey and Fonseca, 2009; Michalski
220 et al., 2019)] emerge. Some initial indications come from mice
221 studies, where virtual reality tasks are associated with partially
222 altered hippocampal dynamics compared with a real-world task
223 (Aghajani et al., 2015), implicating that similar variation in neural
224 computation may occur in humans. The fidelity with which
225 virtual reality settings, including eSports, can emulate aspects of
226 physical sports remains an active field of research. In the case of
227 CSSs, for instance, cycling, a partial convergence between these
228 two worlds (electronic/virtual and physical/real), has already

229 taken place. For instance, commercial systems allow integrating
 230 the use of a stationary bike with the rear wheel placed onto
 231 a motorized roller, whose bidirectional communication with
 232 a computer permits to adjust the resistance and the virtual
 233 landscape (Lazzari et al., 2020). Achieving such convergence
 234 in the case of OSSs is more challenging; however, encouraging
 235 results have been obtained by showing that free throw in
 236 basketball can be improved when subjects are trained in a virtual
 237 reality simulator (Covaci et al., 2012). We address readers to
 238 some recent extensive reviews of this field (Campbell et al., 2018;
 239 Akbaş et al., 2019) for a more dedicated appraisal on the subject
 240 of eSports virtual reality applied to sports. In the future, it will
 241 be interesting to assess neural parameters using an approach
 242 similar to the one used in the rodent study mentioned above,
 243 that is, examining subjects in both environments, to assess for
 244 potential neural similarities/differences in the physical versus
 245 virtual environment.

246 Based on the above premises on sports-specific characteristics,
 247 a body of work has tested the hypothesis that behavioral and
 248 neural processes display variations not only between athletes
 249 and non-athletes but also between athletes from different
 250 sports [e.g., CSS vs. OSS (Kizildag and Tiriyaki, 2012; Wang
 251 et al., 2013b)], or between naive subjects, professional athletes,
 252 and elite athletes, the latter acting as statistical outliers in
 253 terms of sport performance (Aitken, 2004; Hardy et al.,
 254 2017). In the following section, we discuss some recent
 255 work encompassing these levels of investigation and relate
 256 some of these findings to laboratory-based studies of human
 257 motor performance.

259 **READY, SET, GO! ON COGNITIVE AND** 260 **NEURAL FEATURES OF ATHLETES**

263 By definition, in sport contexts, the subjects' performances are
 264 pushed to the limit and as such may teach us critical principles
 265 of human expert behavior (Walsh, 2014). If these performances
 266 are considered as complex (individual and/or interpersonal)
 267 acts, then their study places them at the core of emerging
 268 concepts in neural sciences, including embodied cognition
 269 theories, which state that "cognition should be described in
 270 terms of agent–environment dynamics rather than computation
 271 and representation" (Press, 2020). While shortcomings of such
 272 approach are self-evident, re-evidencing the role of the body
 273 as well as the environment for a deeper understanding of
 274 the brain may have its merits. From an anatomophysiological
 275 point of view, investigating on athletes, like musicians in the
 276 artistic setting (Münste et al., 2002), is informative for learning
 277 about neuroplasticity and maladaptive plasticity resulting from
 278 aberrant training of a specific motor action [mostly through
 279 cross-sectional studies, and some longitudinal studies (Ioannou
 280 et al., 2018; Bravi et al., 2019)].

281 Because sport neuroscience is a relatively new field, a
 282 characterization of cognitive performances and their neural bases
 283 in athletes can be considered still in its infancy. Nonetheless,
 284 what is required to be successful at the highest level in sport is
 285 intuitively a multifaceted set of cognitive abilities. We readdress

286 on this regard interested readers to pertinent reviews (Yarrow
 287 et al., 2009; Nakata et al., 2010) or books (Boecker et al., 2012;
 288 Carlstedt, 2018) and mention here only a few striking instances
 289 linked to the above described categories (athlete vs. non-athlete,
 290 CSS's athlete vs. OSS's athlete, normal vs. elite athlete).

291 Among the behavioral parameters shown to be modified
 292 in athletes, inhibitory control (Benedetti et al., 2020), i.e., the
 293 suppression of inappropriate behavioral responses, is improved
 294 in elite athletes (Brevers et al., 2018), and there is a robust
 295 difference among players of OSS vs. CSS, with the former
 296 outclassing the latter (Wang et al., 2013a). Skilled athletes can
 297 predict the outcome of actions performed by others, based on
 298 the kinematic information inherent in others' actions, earlier and
 299 more accurately than less-skilled athletes (Unenaka et al., 2018).
 300 Also, proactive control was also evidenced to be modulated by
 301 motor skill experiences, with OSS athletes showing higher levels
 302 of efficiency than CSS athletes (Yu et al., 2019).

303 Not surprisingly, some of the behavioral traits of motor
 304 know-how are complemented by anatomical evidence. For
 305 example, corpus callosum is thicker in expert performers
 306 (Gooijers and Swinnen, 2014; Meier et al., 2016). Concerning
 307 neurophysiological data, signals obtained from humans with, e.g.,
 308 electroencephalography (EEG) or functional magnetic resonance
 309 imaging (fMRI), show activity related to movement and motor
 310 expertise, such as reduced brain activation in experts (neural
 311 efficiency) (Guo et al., 2017; Del Percio et al., 2019) and
 312 different threshold to elicit corticospinal facilitation (Fomin
 313 et al., 2010; Fomin and Selyaev, 2011; Wang et al., 2014;
 314 Wright et al., 2018).

315 While EEG has lower spatial resolution with respect to
 316 methods like fMRI and functional near-infrared spectroscopy, it
 317 provides superior temporal resolution and is thus more suitable
 318 for investigating neocortical activation patterns associated with
 319 fast (i.e., in the millisecond range) movements typical of
 320 sports. While other methods such as magnetoencephalography
 321 (Mäkelä, 2014) and event-related optical signal (Gratton and
 322 Fabiani, 1998) have a comparable temporal resolution, EEG-
 323 based investigations have been far more frequently applied
 324 to sport performance. In addition, the rise of portable EEG
 325 devices further offers an invaluable opportunity to study sport
 326 gestures outside laboratory settings (Park et al., 2015; Wang
 327 et al., 2019). We thus restrict our focus on some relevant
 328 EEG studies. The most common approaches are based on
 329 comparisons such as preperformance vs. movement execution,
 330 good vs. bad performance, expert vs. novice, competitive vs. non-
 331 competitive athletes, disabled vs. non-disabled athletes, baseline
 332 vs. learning, and practice vs. competition. Two main categories
 333 of movement responses are usually investigated in EEG studies
 334 of motor performance, namely, movement-related potentials,
 335 including Bereitschaftspotential (readiness potential) and motor
 336 potential, and action-monitoring potentials, such as error-
 337 related negativity (Carlstedt, 2018). A well-known frequency-
 338 domain manifestation of movement includes the Mu rhythm,
 339 a decrease of alpha band and beta band power occurring in
 340 the sensorimotor regions of the neocortex during movement
 341 preparation (Jenson et al., 2020), and OSS athletes (karate
 342 and fencing) compared to control subjects display reduced

343 alpha band activity even during simple upright standing (Del
 344 Percio et al., 2009). Reduced activity in the alpha band has
 345 been reported in CSS athletes (cyclists) as well, which would
 346 suggest that enhanced neural efficiency does not depend on the
 347 type of OSS or CSS sport category practiced (Ludyga et al.,
 348 2015). In contrast, a bilateral increase in parietal areas has
 349 been reported in football players during action observation (Del
 350 Percio et al., 2019). Within the time domain of EEG signals,
 351 motor expertise (fencers) has been linked to altered event-
 352 related potentials and faster stimulus discrimination during go-
 353 no-go tasks (Di Russo et al., 2006). Faster reaction time is
 354 associated with shorter readiness potential in athletes (baseball
 355 players) during go trials, while in no-go trials, they display
 356 an augmented P300 amplitude in the frontal regions, implying
 357 that improved stimulus responses depend on faster response
 358 selection and more robust inhibition (Nakamoto and Mori,
 359 2008). In a similar fashion, other OSS experts (table tennis player)
 360 exhibit superior response inhibition compared to non-athletes
 361 (Yu et al., 2019).

362 Growing evidence suggests that baseline cognitive ability
 363 could be used to predict future achievements in sports, and
 364 studies have shown that both core and higher-level executive
 365 functions predict the success of athletes (Vestberg et al., 2012,
 366 2017; Mangine et al., 2014). The level of expertise is also expressed
 367 by a sort of “immunity” against distractive stimuli in elite
 368 athletes: novice athletes are affected strongly by distracting tasks,
 369 whereas experts are shielded against this distraction, indicating
 370 highly automatic performance (French et al., 1995; Gray, 2004;
 371 Yarrow et al., 2009).

372 Interrogating neural networks in humans implies limited
 373 access to cellular, spiking data *in vivo*, excluding extracellular
 374 recordings during neurosurgeries, and even then, the role
 375 played by different classes of neurons can only be indirectly
 376 inferred. Besides monitoring the activity of brain networks,
 377 to determine a causal role of a given neural pattern for
 378 performance, manipulation techniques, such as transcranial
 379 magnetic stimulation and transcranial direct current stimulation
 380 (tDCS), are advancing rapidly from clinical settings to sport
 381 (Goodall et al., 2014; Edwards et al., 2017; Gazerani, 2017).
 382 Interestingly, such methods provide an opportunity to improve
 383 sport performance. Endurance performance is increased in
 384 recreationally active participants after anodal, but neither
 385 cathodal nor sham, bilateral stimulation of motor cortices,
 386 and this effect is associated with increased corticospinal
 387 excitability of the knee extensor muscles and reduced perception
 388 of effort (Angius et al., 2018). Aside from ethical aspects
 389 associated with the possibility of stimulation techniques to
 390 become part of enhancement tools known as neurodoping
 391 (Davis, 2013; Kamali et al., 2019), and the fact that the long-
 392 term effects of brain stimulation are unknown, the possibility
 393 of increasing performance by refining brain stimulations
 394 methods is an exciting, although controversial, area of research.
 395 Technically, major limitations of current methods are the coarse
 396 spatial resolution and that the stimulation is not cell type-
 397 specific. Hence, efforts to improve our understanding of the
 398 neurophysiology could help develop more efficient approaches
 399 in sport settings.

400 For both monitoring and stimulating neural activity, animal
 401 models offer the opportunities to dissect, within a reverse
 402 engineering approach, brain circuits to determine the causal role
 403 of specific patterns and develop novel neurotechnologies well
 404 beyond the state of the art available in humans. In the following
 405 section, we discuss examples from animal research that could
 406 contribute, from a conceptual and/or a methodological stance, to
 407 gain a more fine-graded understanding of the neuronal basis of
 408 athletic performance.
 409

410 OBSERVING AND HACKING THE 411 ANIMAL BRAIN DURING MOTOR 412 BEHAVIOR 413

414 Songbirds (Clayton, 2019), rodents (Makino et al., 2017; Hwang
 415 et al., 2019; Quarta et al., 2020; Sauerbrei et al., 2020, *preprint*
 416 *article*), and non-human primates studies (Churchland et al.,
 417 2012) provide valuable insights into the neurophysiology of
 418 motor skills; however, sport science has paid relatively little
 419 attention to these mechanisms of expert behavior. For example,
 420 neural recordings from finches have been classically used to
 421 investigate the dynamics of motor learning by imitation (Roberts
 422 et al., 2012), which is a learning approach at the core of
 423 sport performances in developing athletes (Unenaka et al.,
 424 2018). In this regard, a potentially important role is played by
 425 the well-known mirror neurons, discovered in the premotor
 426 and posterior parietal cortex of NHPs (Ferrari and Rizzolatti,
 427 2014). Importantly, mice improved their acquisition of a simple
 428 operant conditioning task by observational learning, with medial
 429 prefrontal cortex and the nucleus accumbens significantly
 430 involved in the acquisition and proper task performance
 431 (Jurado-Parras et al., 2012). Driven by results arising from
 432 animal studies, experiments on the role played by motor
 433 imagery training for sport performance have gained momentum
 434 (Lewthwaite and Wulf, 2010).
 435

436 Research lines on the role played by physical activity for
 437 the homeostasis of neural circuits and behavior are now well
 438 established in rodents. As a notable instance, specific physical
 439 exercise protocols in rodents, for example, running, have been
 440 repetitively associated with enhanced levels of neuroplasticity and
 441 improved behavioral learning (van Praag et al., 1999; Kobilov et al.,
 442 2011; Li and Spitzer, 2020).

443 Rodents have recently gained momentum to investigate
 444 certain aspects of motor performance, and it is now established
 445 that cellular actors including neurotrophins such as brain-
 446 derived neurotrophic factor (BDNF) mediate motor skill learning
 447 (Arango-Lievano et al., 2019). For example, it was demonstrated
 448 that BDNF signaling is necessary for the behavioral effects
 449 of tDCS to occur (Fritsch et al., 2010). Importantly, in the
 450 same work, the authors extended their findings to humans,
 451 demonstrating a limited effect of tDCS stimulation in subjects
 452 with a polymorphism known to reduce [18–30% (Egan et al.,
 453 2003; Chen et al., 2006)] the secretion of BDNF, implying that
 454 the effects are likely mediated by this type of cellular signaling in
 455 humans as well (Fritsch et al., 2010). In any case, the relationship
 456 between motor behavior and BDNF signaling has been under

Q12

intense scrutiny in both rodents (Boger et al., 2011; Besusso et al., 2013) and humans (Grégoire et al., 2019).

Selected types of sensorimotor transformations, such as locomotion, are beginning to be understood at the cellular level in rodents (Ferezou et al., 2007; Papale and Hooks, 2018). The investigation of the neural dynamics subserving more complex movements such as reaching and grasping, which form the motor building blocks for many sports gestures, is classically studied in NHPs and more recently adapted for rodents (Guo et al., 2015). In rodents, which allow precise neurophysiological dissection, thanks to the availability of powerful genetic engineering and optical methods, a cortical characterization has been recently made available (Guo et al., 2015; Wang et al., 2017; Quarta et al., 2020, *preprint article*; Sauerbrei et al., 2020).

The relevance of neocortical circuits for manipulative behaviors in rodents has been classically established *via* lesion or pharmacological approaches. For instance, local anesthetics injected in the forelimb area of mice were shown to alter movement parameters (Estebanez et al., 2017; Galinanes et al., 2018). Also, recent evidence shows a direct involvement of the facial area of the rabbit motor cortex in the acquisition and performance of conditioned eyeblinks (Ammann et al., 2016).

Technological development, most notably *in vivo* optogenetics, opened the opportunity to perform cell type-specific, reversible, and temporally precise (in the millisecond range) excitation or inhibition of neurons in behaving animals, at times with a spatial resolution allowing to dissect the specific role of a given cellular (sub) population (Fenno et al., 2011; Chen et al., 2018).

Using such a method for the study of motor behavior, it was, for instance, discovered that inhibitory neurons in the contralateral sensorimotor cortex command specific phases of reaching and grasping in the mouse (Guo et al., 2015), that cerebellar anterior interposed nucleus exerts control over the speed of reaching movement (Becker and Person, 2019), and that perturbing the thalamocortical communication impairs forelimb movement kinematics in a frequency-dependent manner (Sauerbrei et al., 2020).

Nevertheless, a neuroanatomical limit of comparison of motor circuits between rodents and primates is the corticomotoneuronal pathway, which is thought to serve fine movements in NHPs and humans (Fetz et al., 1989). While tract-tracing experiments could evidence a direct corticospinal connection in rodents with concurrent physiology consistent with corticospinal cells (Sheets et al., 2011; Oswald et al., 2013), current evidence indicates no functional contacts between corticospinal axons and motoneurons in adult rodents (Alstermark et al., 2004). In their seminal work, Alstermark and colleagues also demonstrated that in rodents this pathway is polysynaptic, with additional cell types located in the reticular formation, as well as due to segmental interneurons in spinal cord (Alstermark et al., 2004). A direct corticomotoneuronal pathway could be recently maintained in adult mice *via* genetic engineering, and when this tract is present, their manual dexterity is improved (Gu et al., 2017).

On the other side, a major effort has been made to translate advanced tools for neural circuit interrogation

from phylogenetically lower species such as rodents to NHPs (Galvan et al., 2017; O'Shea et al., 2017). Remarkable results have been achieved; for instance, it was demonstrated that dendritic activity recorded optically from the motor cortex of monkeys transfected to express a fluorescent activity reporter in excitatory neurons could reliably be employed to predict the direction of the arm movement [Trautmann et al., 2019, *preprint article*]. Manipulating cerebellar neurons *via* optogenetics could drive saccade movements (El-Shamayleh et al., 2017), while performing similar recordings and stimulation in the motor cortex of marmoset monkeys has been employed to investigate the neural dynamics of arm movements (Ebina et al., 2018, 2019).

In summary, animal models, in particular, rodents and NHPs, offer the opportunity to investigate mechanistic aspects of behavioral expertise (Mayse et al., 2014).

OF MICE AND MEN: EXAMPLES TOWARD ANIMAL MODELS OF SPORT

While we acknowledge that not all aspects of sport performance will benefit from inputs from animal neurophysiology of motor behavior, we discuss below successful examples that may spark discussion across disciplines.

Optimal Arousal for Optimal Performance

A remarkable example of successful translation of concepts from animal studies to human performance is represented by the pioneering work by Yerkes and Dodson on the optimal level of arousal needed to achieve the highest performance. In their study, rats were requested to solve an easy or a difficult task and were given a motivational varying cue of different intensity based on errors they made during training (Yerkes and Dodson, 1908). Upon increasing stimulus intensity, the performance of the rats increased monotonically for easy or well-learned task, while for a task considered difficult the performance decreased abruptly when the stimulus intensity exceeded a certain threshold. The experimental data on the latter fitted well a parabolic function and led to the formulation of the Yerkes-Dodson law, stating an inverted-u relationship between arousal and behavioral performance. Since then, similar conclusions were achieved in humans, including in sport settings, and this relationship is related to the well-known phenomena of clutching and of choking under pressure (Kamata et al., 2002; Yu, 2015).

The Playing Rats

Sport, even in its most competitive settings, has a hedonic motivation. It has been long thought that the latter is an almost exclusive trait of humans; however, recent evidence suggests that even rodents engage in a task “just for fun of it,” Brecht and collaborators were able to demonstrate that rats can play hide-and-seek with a human (Reinhold et al., 2019). Rats quickly learned the game and learned to alternate between hiding versus seeking

Q13

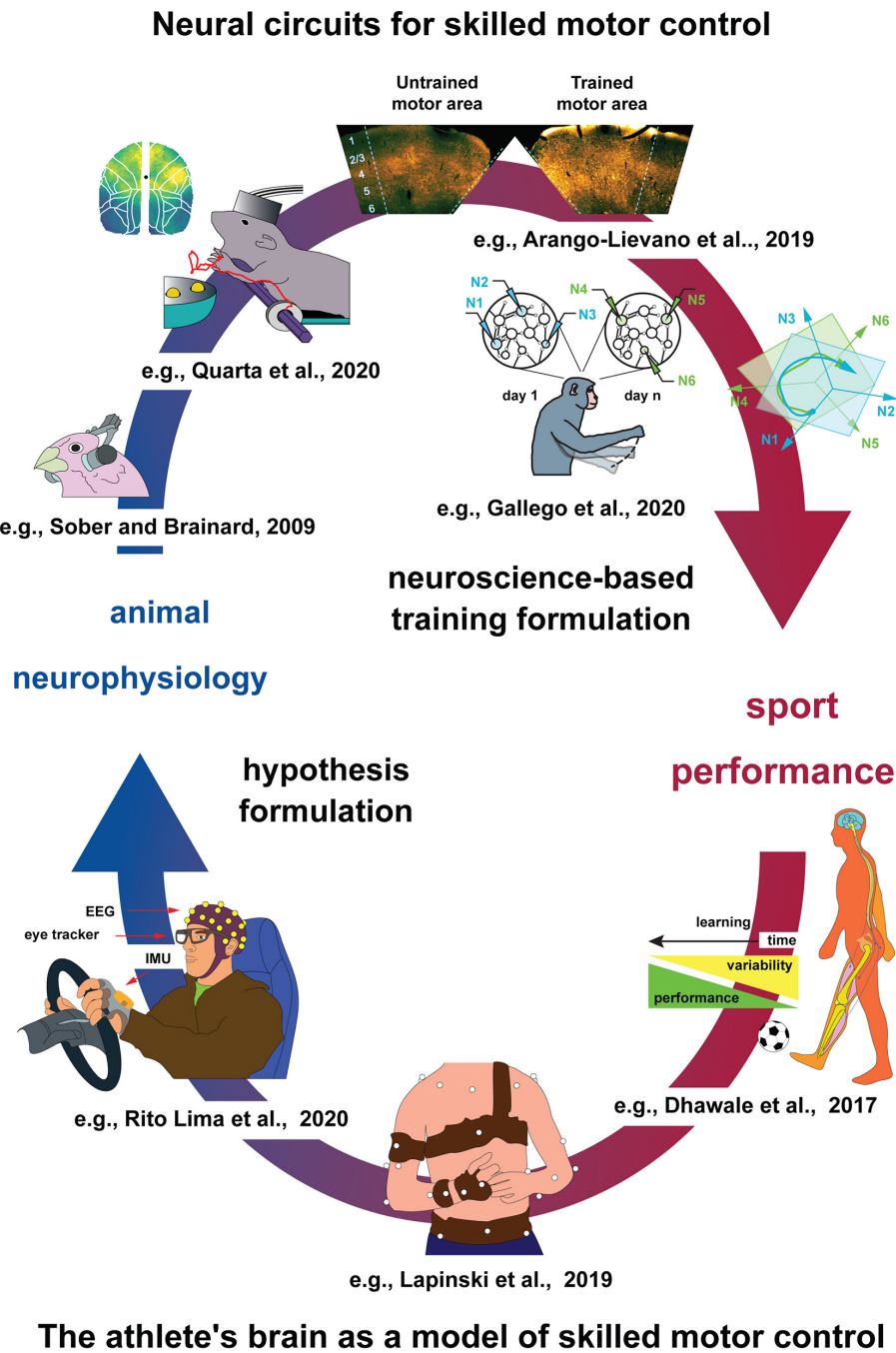


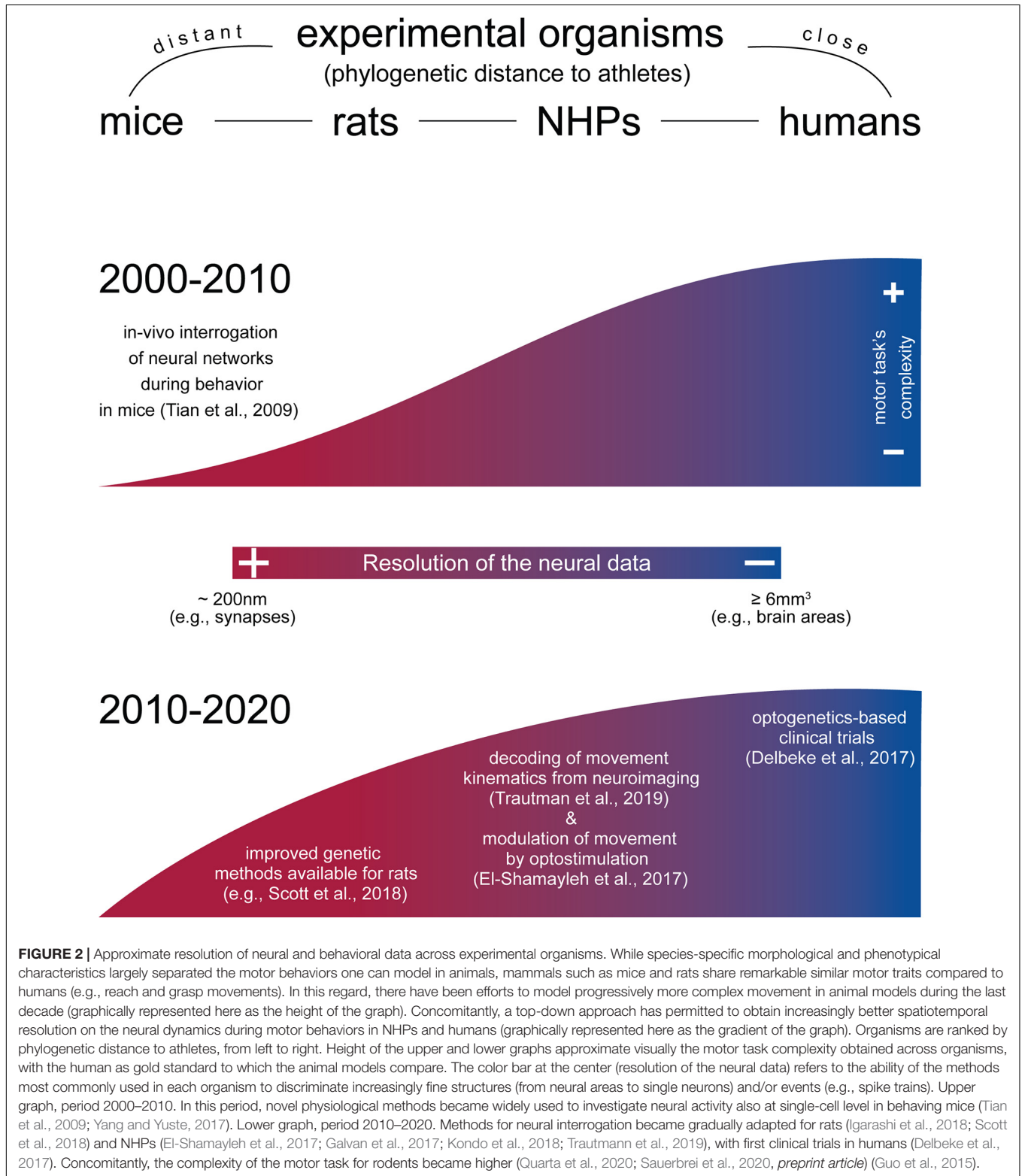
FIGURE 1 | Proposed cycle of information sharing between animal neurophysiology and sport science. *Top: Animal models of skilled motor control.* From left to right. Considering skilled behavior largely depends on commands issued by the nervous system, efforts to shine light on such mechanisms may lead us to a better understanding of sport performance. Animal models allow dissecting such mechanisms in much higher detail, compared to humans. For example, selected neuronal mechanisms for motor learning by imitation can be investigated already in phylogenetic older species such as birds [e.g., finches (Sober and Brainard, 2009; Garst-Orozco et al., 2014; Sober et al., 2018)]. The neural control of limb movements in mammals is increasingly investigated in laboratory rodents, especially rats and mice, which employ powerful optical and genetic tools for cell type-specific analysis of neural dynamics, while permitting to carry out increasingly complex motor tasks (Guo et al., 2015; Ash et al., 2017; Arango-Lievano et al., 2019, *preprint article*; Quarta et al., 2020, *preprint article*). The closest experimental organisms to humans, non-human primates (NHPs), have the highest manual dexterity and still allow single-cell-level interrogation of neural activity during skilled motor control (Gallego et al., 2020). *Bottom: The athlete's brain as a model of skilled motor control.* From right to left. By integrating both concepts and technologies originally developed in animals, advanced analysis of human sport performance metrics allows multivariate data analysis and hypothesis formulation to be tested in athletes, also in laboratory settings involving behavioral tasks mimicking sport gesture (Dhawale et al., 2017), using marker-based and, increasingly, markerless approaches (Mathis et al., 2018; Lapinski et al., 2019). Movement data, acquired also *via* inertial measurement units and eye trackers, are complemented by, e.g., EEG, which permit coarse-resolution level analysis of neural networks involved in skilled motor control (Rito Lima et al., 2020), serving as a potential starting point for animal studies.

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685 roles, with specific neural activity patterns emerging in the
 686 prefrontal cortex. Clearly, these findings have important
 687 implication for the goal of modeling sport (with hide-and-
 688 seek being an unusual, yet a candidate Olympic sport)

performance in animals, including potential next steps such
 as optogenetic experiments to alter the activity in the prefrontal
 cortex to determine the necessity of specific patterns for
 behavioral performance.



799 Motor Skills of an Olympic Mouse: Too 800 Far Reaching?

801 It seems intuitive to reject the hypothesis that a trained
802 animal may be informative about how motor skills emerge in
803 sportspeople, possibly because “being the best of the best as an
804 athlete encompasses more than having a very high level of motor
805 skill after a lot of training” (Krakauer, 2017). However, this limit
806 may be due not to biology *per se* (Grandin and Whiting, 2018)
807 but is rather associated with the common research methodology
808 concerning motor control in animals, which tends to focus on
809 population average (mean motor performance) rather than on
810 the upper statistical outliers (elite motor performance). As a
811 potentially relevant point, genetic tools and selective breeding
812 (e.g., for longer legs) available in animal neurophysiology allow
813 to perform hypothesis testing difficult to perform in humans (e.g.,
814 the importance of a genetic background), informing us about the
815 relative importance of specific traits for motor performance. This
816 intended mutual information exchange is drawn as a self-feeding
817 cycle (Figure 1).
818

819 DISCUSSION: THE ROADMAP FOR A 820 TRANSDISCIPLINARY DIALOG

821 To stimulate a transdisciplinary dialog, a back-translation of
822 sport sciences findings to animal models and the evaluation
823 of comparability between animal models of a given sport and
824 athletes will require several intermediate steps. Behaviorally, non-
825 invasive tools developed in animal research will most likely be
826 employed in sport settings anytime soon, in particular methods
827 for markerless tracking based on machine learning approaches,
828 which evidence that detailed information on motor behavior can
829 be extracted from animal and humans with the same approach
830 (Mathis et al., 2018).
831

832 Encouragingly, in recent years, there has been a successful
833 effort to translate neurophysiological techniques that allow cell
834 type-specific interrogation from rodents to NHPs. Thus, at least
835 in theory, it is procedurally feasible to extend this range of
836 techniques in humans as well. As a notable instance, in the
837 last 10 years, optogenetics has moved from rodent to NHPs for
838 basic neurophysiology studies and has entered preclinical trials
839 in human patients (Simunovic et al., 2019; Figure 2).
840

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855 An intriguing intermediary step could be the opportunity
856 of investigating the dynamics of human neurons *in vivo* by
857 transplanting induced pluripotent stem cell-derived neurons
858 into the mouse brain (Real et al., 2018). While an investigation
859 on expert motor behavior is yet prospective, this type
860 of xenotransplants could inform us about the mechanisms
861 underlying the neural bases of (sport) performance in a subject-
862 specific manner.
863

864 Overall, investigating athletes and trained animals with a
865 logic comparable to early cognitive neuroscience studies on
866 neurologically impaired individuals (Agis and Hillis, 2017) will
867 not only teach us about general principles of behavior but
868 could rather provide a bedrock for novel and more efficient
869 training and rehabilitation methods (Reiman and Lorenz, 2011).
870 This would be conceptually similar to a main use of animal
871 models in biomedical research, that is, to inform us about the
872 mechanisms through which neurodegenerative disorders affect
873 neural circuits and behavior and to test potential new treatments
874 and/or neuroprotective agents, such as neurotrophic factors,
875 physical exercise, and, increasingly, motor expertise (Cai et al.,
876 2014; Quarta et al., 2015, 2018; Nie and Yang, 2017; Dawson et al.,
877 2018; Ng et al., 2019; Tsai et al., 2019).

878 Thus, an exciting dawn of opportunities lies ahead, which
879 will allow to control, and possibly improve, movements in
880 human subjects extending the limit of human performance
881 (Triviño, 2014).
882

883 DATA AVAILABILITY STATEMENT

884 The original contributions presented in the study are included
885 in the article/supplementary material, further inquiries can be
886 directed to the corresponding author/s.
887

888 AUTHOR CONTRIBUTIONS

889 EQ and DM: concept development, figure preparation,
890 manuscript preparation, and manuscript proofreading. EC and
891 RB: concept development, figure preparation, and manuscript
892 proofreading. All authors contributed to the article and approved
893 the submitted version.
894

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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