

The effects of reward and punishment on motor skill learning

Chen, Xiuli; Holland, Peter; Galea, Joseph

DOI:

[10.1016/j.cobeha.2017.11.011](https://doi.org/10.1016/j.cobeha.2017.11.011)

License:

Creative Commons: Attribution-NonCommercial-NoDerivs (CC BY-NC-ND)

Document Version

Peer reviewed version

Citation for published version (Harvard):

Chen, X, Holland, P & Galea, J 2018, 'The effects of reward and punishment on motor skill learning', *Current Opinion in Behavioral Sciences*, vol. 20, pp. 83-88. <https://doi.org/10.1016/j.cobeha.2017.11.011>

[Link to publication on Research at Birmingham portal](#)

General rights

Unless a licence is specified above, all rights (including copyright and moral rights) in this document are retained by the authors and/or the copyright holders. The express permission of the copyright holder must be obtained for any use of this material other than for purposes permitted by law.

- Users may freely distribute the URL that is used to identify this publication.
- Users may download and/or print one copy of the publication from the University of Birmingham research portal for the purpose of private study or non-commercial research.
- User may use extracts from the document in line with the concept of 'fair dealing' under the Copyright, Designs and Patents Act 1988 (?)
- Users may not further distribute the material nor use it for the purposes of commercial gain.

Where a licence is displayed above, please note the terms and conditions of the licence govern your use of this document.

When citing, please reference the published version.

Take down policy

While the University of Birmingham exercises care and attention in making items available there are rare occasions when an item has been uploaded in error or has been deemed to be commercially or otherwise sensitive.

If you believe that this is the case for this document, please contact UBIRA@lists.bham.ac.uk providing details and we will remove access to the work immediately and investigate.

The effects of reward and punishment on motor skill learning

Xiuli Chen^{1*}, Peter Holland^{1*}, Joseph M. Galea¹

¹ School of Psychology, University of Birmingham, UK.

* Authors contributed equally

Corresponding author

Joseph M. Galea

Email: j.galea@bham.ac.uk

Abstract

Motor skill learning consists of improvement in two main components: action selection and action execution. Although sports' coaching identifies reward and punishment as having important but dissociable effects for optimising motor skill learning, it is unknown whether they influence selection and/or execution. In addition, whilst current laboratory-based motor skill tasks have investigated the impact of reward and punishment on learning, they have failed to distinguish between improvements in these components. To examine how reward and punishment may impact selection and execution, we discuss their effects in cognition and motor control. We highlight several similarities between these results and those reported in sports coaching and laboratory-based motor skill learning. However, to fully understand these links, we believe novel laboratory-based motor skill learning tasks that allow the effects of reward/punishment on selection and execution to be examined independently are required.

Highlights

- Reward and punishment have dissociable effects on motor skill learning.
- Motor skill learning involves action selection and action execution.
- Other disciplines reveal reward/punishment effects on selection and execution.
- Reward/punishment effects on selection and execution in motor learning are unknown.
- New motor learning tasks must separate selection and execution.

36 **Introduction**

37 Humans possess a remarkable ability to learn new motor skills [1]. Underlying this ability is a
38 complex network of systems mediated by numerous different brain regions [2]. The sensitivity of each
39 of these systems is likely differentially modulated by the rewards and punishments that arise as a
40 result of motor output [3,4]. Although there are various heuristic rules in the field of sports coaching
41 which are thought to represent the optimal strategies for implementing reward and punishment [5], the
42 scientific basis for these is not clear. In this opinion article, we examine the manner in which reward
43 and punishment could affect specific components of motor skill learning and propose future
44 experiments that may help elucidate some of the many remaining questions.

45

46 **What is motor skill learning?**

47 To begin with, we outline our definition of skill (Box 1). Motor skill learning is a relatively slow
48 process that results in improvements in performance above baseline levels [2]. This improvement can
49 be achieved through two main components. The first is through developing an overall understanding
50 of the task environment in which learning what-to-do-when is critical (knowledge of facts), which we
51 refer to as action selection [6]. The second is through increasing precision of the selected action,
52 referred to here as action execution and measured by motor acuity [6,7] (Figure 1).

53

54 ***Box 1: Components of motor skill learning***

55 *Although the term ‘motor skill learning’ is widely used in the literature, the exact meaning is unclear.*
56 *One point of general agreement is that the learning of a motor skill should result in a shift of the*
57 *speed-accuracy trade-off of performance of that skill [28]. However, such improvements could be*
58 *made in multiple ways. Although in this article we have made a distinction between ‘action selection’*
59 *and ‘action execution’, these may not be two entirely separable processes. Diedrichsen and*
60 *Kornysheva (2015) [29] refer to an intermediate stage between selection and execution that*
61 *incorporates the use of combinations of motor ‘chunks’ into skilful actions. It remains to be seen how*
62 *the principles described in the current article apply to this process with this being a vital area of*
63 *future research. It is also important to note that even in the action selection stage we refer to here*
64 *may be comprised of more than one system. In the field of cognition, both a model-free and model-*
65 *based system are proposed [18]. For simplicity, when we refer in this article to ‘action selection’ we*
66 *do not attempt to discriminate between these two systems or make claims about the implicit or explicit*
67 *nature of the selection of actions. For a true understanding of the effects of reward and punishment*
68 *on motor skill learning, researchers should attempt to at least address which of these many processes*
69 *the feedback may be affecting.*

70

71 **Reward and punishment within action selection**

72 Thus, part of skill learning depends on knowledge-based selection of the correct actions [6], e.g.
73 learning to select a specific shot in basketball at the correct point in the game (Figure 1). Although
74 action selection processes have rarely been studied in the context of complex motor tasks, there is a
75 vast literature which probes action selection during cognition-based paradigms. Using a broad
76 spectrum of tasks (economic decision-making, two-armed bandit, go/no-go, reversal learning), it has
77 been shown that human participants can treat reward and punishment as distinct categories of events

78 [8]. However, behavioural differences between reward and punishment are mainly observed during
79 the process of choosing an action among a predefined set of options (e.g., economic decision-making
80 task) [9-11], rather than the process of learning/estimating action values through trial-and-
81 error/reinforcement learning (e.g., two-armed bandit task) [12].

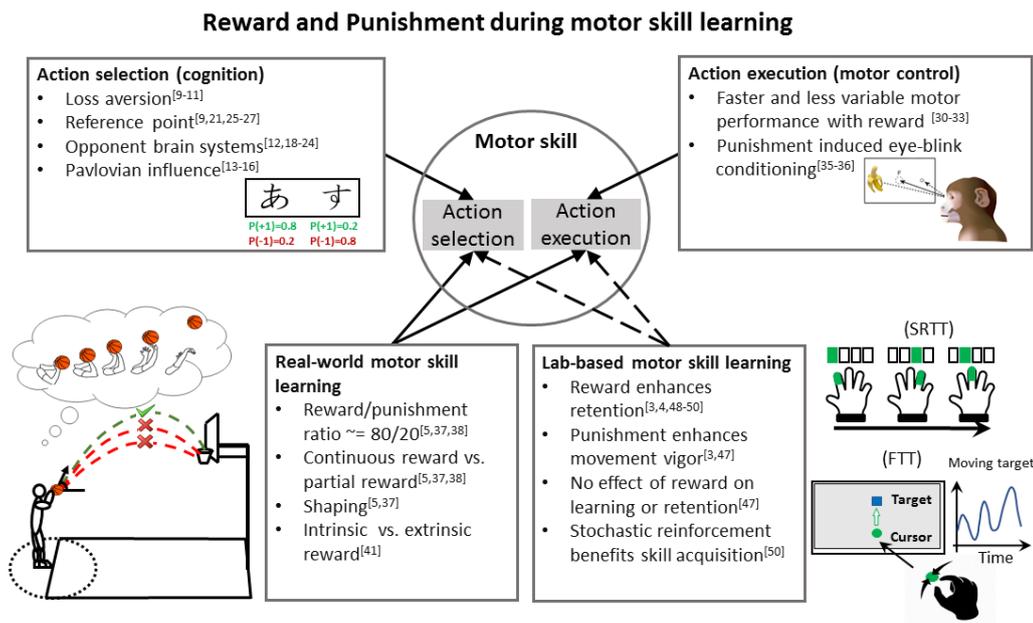
82
83 For example, within economic decision-making participants consistently display loss aversion
84 whereby they tend to avoid choices that lead to loss, even when accompanied with the opportunity to
85 receive equal or larger gains [9-11]. In addition, economic and go/no-go decision-making tasks have
86 revealed that action selection is biased by inherent Pavlovian biases which promote action towards
87 reward and inaction in the face of punishment [13-16]. As a result of these biases, participants find it
88 significantly harder to choose options which involve initiating an action to avoid punishment or
89 inhibiting an action to obtain reward [14].

90
91 In contrast, healthy participants exhibit similar reward and punishment-based learning during trial-
92 and-error/reinforcement learning tasks [12,17]. Despite this, reward and punishment appear to activate
93 partially separable brain systems [18]. Whereas reward engages dopaminergic frontostriatal circuits
94 [19,20], punishment is associated with activity changes in both the striatum and insula [12,21-24]. To
95 complicate matters, the definition of reward and punishment is highly dependent on a participant's
96 previous experience, referred to as their reference point [9,21]. For example, within a punishment
97 context, successful punishment avoidance can be coded as a reward both behaviourally and at a neural
98 level where the brain's response shifts from the anterior insula (associated with punishment) to the
99 ventral striatum (associated with reward) [25]. The value and importance of this reference point can
100 be altered by task instructions and feedback [25-27].

101
102 **Reward and punishment within action execution**

103 Although a complex story, it is clear that reward and punishment can have dissociable effects on
104 action selection, but what about action execution? The improvement in action execution (motor
105 control) is generally characterised by a shift in the speed-accuracy trade-off (Box 1) [28,29], i.e., an
106 ability to perform the action both faster and more accurately. It has been shown that for saccades, the
107 potential of reward can induce shifts in the speed-accuracy trade-off in the absence of learning [30-
108 32]. Specifically, in monkeys and humans, saccades made in rewarded directions show decreased
109 variability and latencies despite increased velocities [30-33]. These temporary improvements driven
110 by prospective reward were muted in Parkinson's disease, suggesting an important role for
111 dopaminergic circuits in this effect [33]. Despite a paucity of research, it appears that similar reward-
112 based shifts in the speed-accuracy trade-off are observed in reaching movements [34]. Hence, if
113 action execution improvement is measured by a shift in the speed accuracy trade-off, do we need to

114 redefine this to include a shift outside of the normal range, including reward, and one that persists
 115 even when the reward is removed? At present it is unknown whether punishment has a similar effect
 116 on action execution. However, in the field of eye-blink conditioning, a correctly timed response is
 117 acquired in order to avoid punishment [35,36], suggesting punishment can lead to timing-based
 118 improvements in action execution. In spite of this work, indicating that reward and punishment can
 119 individually affect some aspects of action execution, it is currently unknown whether reward and
 120 punishment have dissociable effects on action execution.
 121



122
 123 **Figure 1: The effects of reward and punishment on motor skill learning.** Motor skill
 124 learning consists of improvement in two components: action selection and action execution
 125 (centre). A vast literature that probes action selection during simple cognition-based
 126 paradigms has shown dissociable effects of reward and punishment (top-left). In terms of
 127 action execution, studies have shown that potential reward enables participants to perform an
 128 action both faster and more accurately (top-right). Although this evidence shows that reward
 129 and punishment influence both action selection and execution when examined independently,
 130 it remains unclear how this relates to motor skill learning. Real-world motor skill learning
 131 requires both selection and execution (bottom-left). For example, an ideal basketball shot
 132 requires both selecting the best aim angle and optimally executing the chosen angle (bottom-
 133 left). Despite sports coaching highlighting the importance of reward- and punishment-based
 134 feedback, it is currently unknown whether they influence selection, execution or both. In
 135 addition, current lab-based motor skill learning tasks (bottom-right) have investigated the
 136 influence of reward and punishment-based feedback on task performance however, they have
 137 failed to distinguish improvements in these two components. We believe that novel
 138 laboratory-based motor skill learning tasks that enable the effects of reward and punishment
 139 on selection and execution to be examined independently are required.
 140

141

142 **Real world motor skill learning**

143 Although there is evidence that reward and/or punishment influences both action selection and
144 execution when examined independently, it remains unclear how this relates to motor skill learning.
145 Sports' coaching provides a good example of the perceived importance of reward and punishment
146 feedback for motor skill learning within a real-world environment. Coaching manuals describe how a
147 coach should use a combination of reward and punishment to optimise changes in an athlete's
148 performance [5]. In fact, numerous strategies are proposed for implementing reward and punishment
149 within coaching [5,37,38] which as evidence provide a short description of classic operant
150 conditioning literature [39]. However, little laboratory-based research has attempted to directly test
151 these theories.

152
153 In terms of reward, there is a belief that it should be provided immediately with every instance of the
154 behaviour being rewarded in the early stages of learning (continuous reward). After the bond between
155 good behaviour and reward is formed, reward should be provided stochastically (partial reward)
156 [5,37,38]. In addition, skills should be broken into segments with reward being based on small
157 improvements of these segments (shaping) [5,37]. One interesting question is whether these
158 behavioural improvements achieved by reward-based shaping have underlying similarities with the
159 reward-driven shifts in speed-accuracy trade-offs [33,40]? A clear distinction is also made between
160 intrinsic (enjoyment/satisfaction) and extrinsic (trophies, money) reward, with it being suggested that
161 external reward can have positive and negative effects on intrinsic reward [41].

162
163 With regard to punishment, it should only be provided sparingly (80% reward - 20% punishment rule)
164 [5,37,38]. Although there is agreement that punishment can be effective in decreasing unwanted
165 behaviour, it can also have undesirable side effects. For example, if used excessively it can promote
166 the fear of failure which can in turn increase the likelihood of failure (choking) [5,37,38]. It is
167 possible that the principles of loss aversion and Pavlovian biases described in the field of decision-
168 making [9-11] are highly relevant to these coaching principles. In addition, rather than using aversive
169 punishment (adding something aversive) a more effective form of punishment is 'response cost'
170 (removal of something positive) [37,38]. Again links between this coaching rule and the different
171 ways in which punishment is perceived in cognition (substantive punishment vs. omission of reward)
172 [21] have yet to be studied.

173
174 Therefore, if motor skill learning involves improvements in both action selection and execution [6],
175 then the fundamental question is how these observations during real-world motor skill learning,
176 regarding the optimal implementation of reward and punishment, relate to the work carried out within
177 the domains of action selection (cognition) and action execution (motor control) (Figure 1)? Does

178 reward- and punishment-feedback purely affect an athlete's ability to select the optimal action or can
179 they also enhance an athlete's capacity to execute the selected action with more precision? To answer
180 these questions, we believe that laboratory-based motor skill learning tasks need to be developed that
181 allow the influence of reward and punishment on selection and execution to be examined
182 independently.

183

184 **Laboratory-based motor skill learning**

185 Surprisingly few studies have investigated the influence of reward and punishment during laboratory-
186 based motor skill learning. Although there is work which has examined the effects of reward and
187 punishment in motor adaptation [42-46], we will not discuss these here as adaptation is generally
188 thought as an independent mechanism to motor skill learning [2,29].

189

190 First, using a serial reaction time task (SRTT) monetary punishment was found to decrease reaction
191 times globally whereas reward led to specific improvements in learning of the sequence [3]. fMRI
192 revealed that reward related improvements in procedural learning was associated with activity in the
193 striatum, whereas punishment led to activation in the inferior frontal gyrus and the insula, similar to
194 what has been described in cognitive decision-making [12,19]. In a force tracking task (FTT) it was
195 found that, in comparison to both punishment and neutral feedback, monetary reward led to enhanced
196 retention and offline memory gains [4]. In contrast, Steel et al., (2016) [47] found little effect of
197 reward on learning or retention in either a FTT or the SRTT. In addition, the authors found
198 punishment led to faster reaction times in the sequence learning blocks, which contrasts to the non-
199 sequence-related speeding of reaction times found by Wächter et al., (2009). In the FTT [47],
200 punishment led to an impairment of performance assessed before and after training which again
201 diverges from the results of Abe et al., (2011) [4].

202

203 Finally, using a sequential visual isometric pinch task (SVIPT) it has been shown that reward-based
204 improvements in motor skill behaviour are associated with a frontostriatal circuit [48,49], and are
205 more beneficial if reward is provided in a stochastic manner [50]. This suggests a possible link to the
206 'partial reward' approach to coaching [5,37,38] and the involvement of the same reward-related brain
207 areas involved in cognition-based action selection [22,23].

208

209 Although interesting, it is difficult to make any firm conclusions regarding the influence of reward
210 and punishment in laboratory-based motor skill learning. We believe this is due to the use of a range
211 of experimental tasks which are loosely termed 'motor skills' without a great deal of understanding as
212 to what exactly each task was measuring. Each of these tasks could involve improvements in both
213 action selection and execution [6]. As these studies examined the impact of reward and punishment

214 during a participant's initial encounter with a skill, it is unclear to what degree these improvements
215 occurred through action selection and/or execution. Therefore, such experimental designs are
216 currently unable to determine the exact process reward and punishment are influencing.

217

218 **Future direction**

219 In order to provide a clearer understanding of how reward and punishment influence motor skill
220 learning, we believe laboratory-based tasks need to be developed that specifically isolate the action
221 selection and execution parts of motor skill learning. We accept that this is not an easy challenge as
222 skill learning involves the interplay between these two components, and the balance of the two may
223 vary considerably as learning progresses [29]. However, approaches which enable measuring the
224 selection and execution process separately [33] or designs in which they are separated in time would
225 help elucidate the process being affected.

226

227 In future, laboratory-based tasks could be developed that encompass two independent stages in which
228 reward and punishment are based on either a participant's ability to select the appropriate action or
229 their capacity to execute that action. For example, an experiment could be centred on the game of golf
230 in which participants aim to select the optimal shot to play, analogous to the role of a caddie, and then
231 attempt to successfully execute that selected action, the role of the golfer. Within this task, the impact
232 of reward and punishment could be compared across scenarios in which participants select and
233 execute the action (caddie + golfer), only select the action (caddie) or only execute the action (golfer).
234 It follows that questions for future work include: how does reward and punishment feedback influence
235 the action selection and execution components of motor skill learning? Is a coach's primary role to
236 provide motivation for increased practise [51], to inform athletes on which actions to perform when
237 [52], to improve the execution of specific components of an action or a combination of all?

238

239 **Conclusion**

240 Although real-world (sports) and laboratory-based motor skill learning is differentially affected by
241 reward and punishment, the results are often difficult to interpret and the underlying mechanism is
242 unknown. We suggest that reward and punishment could be acting on either action selection, action
243 execution or both. We believe the development of novel motor skill learning tasks that allow the
244 impact of reward and punishment on selection and execution to be dissociated will enable a more
245 coherent understanding regarding the effects reward and punishment have on motor skill learning.

246

247 **Conflict of interest statement**

248 All authors declare that we have no conflicts of interest.

249

250 **Acknowledgements**

251 This work was supported by an ERC starting grant to JMG (MotMotLearn: 637488).

252

253 **References**

- 254 1. Krakauer JW, Mazzoni P: **Human sensorimotor learning: adaptation, skill, and**
255 **beyond**. *Curr Opin Neurobiol* 2011.
- 256 2. Shmuelof L, Krakauer JW: **Are we ready for a natural history of motor learning?**
257 *Neuron* 2011, **72**:469-476.
- 258 3. Wachter T, Lungu OV, Liu T, Willingham DT, Ashe J: **Differential effect of reward and**
259 **punishment on procedural learning**. *J Neurosci* 2009, **29**:436-443.
- 260 4. Abe M, Schambra H, Wassermann EM, Luckenbaugh D, Schweighofer N, Cohen LG:
261 **Reward improves long-term retention of a motor memory through induction of**
262 **offline memory gains**. *Curr Biol* 2011, **21**:557-562.
- 263 5. Warren W: *Coaching and motivation: a practical guide to maximum athletic performance*:
264 Reeds wain; 1983.
- 265 6. Stanley J, Krakauer JW: **Motor skill depends on knowledge of facts**. *Front Hum*
266 *Neurosci* 2013, **7**:503.
- 267 7. Shmuelof L, Yang J, Caffo B, Mazzoni P, Krakauer JW: **The neural correlates of learned**
268 **motor acuity**. *J Neurophysiol* 2014, **112**:971-980.
- 269 8. Palminteri S, Pessiglione M: *Opponent brain systems for reward and punishment learning:*
270 *causal evidence from drug and lesion studies in humans*. In *Decision Neuroscience*.
271 Edited by Elsevier; 2017.
- 272 9. Kahneman D, Tversky A: **Prospect Theory - Analysis of Decision under Risk**.
273 *Econometrica* 1979, **47**:263-291.
- 274 10. De Martino B, Camerer CF, Adolphs R: **Amygdala damage eliminates monetary loss**
275 **aversion**. *Proc Natl Acad Sci U S A* 2010, **107**:3788-3792.
- 276 11. Rutledge RB, Smittenaar P, Zeidman P, Brown HR, Adams RA, Lindenberger U, Dayan
277 P, Dolan RJ: **Risk Taking for Potential Reward Decreases across the Lifespan**.
278 *Curr Biol* 2016, **26**:1634-1639.
- 279 12. Palminteri S, Justo D, Jauffret C, Pavlicek B, Dauta A, Delmaire C, Czernecki V, Karachi
280 C, Capelle L, Durr A, et al.: **Critical roles for anterior insula and dorsal striatum**
281 **in punishment-based avoidance learning**. *Neuron* 2012, **76**:998-1009.
- 282 13. Guitart-Masip M, Economides M, Huys QJ, Frank MJ, Chowdhury R, Duzel E, Dayan P,
283 Dolan RJ: **Differential, but not opponent, effects of L-DOPA and citalopram on**
284 **action learning with reward and punishment**. *Psychopharmacology (Berl)* 2013.
- 285 14. Guitart-Masip M, Huys QJ, Fuentemilla L, Dayan P, Duzel E, Dolan RJ: **Go and no-go**
286 **learning in reward and punishment: interactions between affect and effect**.
287 *Neuroimage* 2012, **62**:154-166.
- 288 15. Guitart-Masip M, Chowdhury R, Sharot T, Dayan P, Duzel E, Dolan RJ: **Action controls**
289 **dopaminergic enhancement of reward representations**. *Proc Natl Acad Sci U S A*
290 2012, **109**:7511-7516.
- 291 16. Rutledge RB, Skandali N, Dayan P, Dolan RJ: **Dopaminergic Modulation of Decision**
292 **Making and Subjective Well-Being**. *J Neurosci* 2015, **35**:9811-9822.
- 293 17. Frank MJ, Seeberger LC, O'Reilly R C: **By carrot or by stick: cognitive reinforcement**
294 **learning in parkinsonism**. *Science* 2004, **306**:1940-1943.
- 295 18. Daw ND, Kakade S, Dayan P: **Opponent interactions between serotonin and**
296 **dopamine**. *Neural Netw* 2002, **15**:603-616.

- 297 19. O'Doherty J, Dayan P, Schultz J, Deichmann R, Friston K, Dolan RJ: **Dissociable roles**
298 **of ventral and dorsal striatum in instrumental conditioning.** *Science* 2004,
299 **304:452-454.**
- 300 20. Shiner T, Seymour B, Wunderlich K, Hill C, Bhatia KP, Dayan P, Dolan RJ: **Dopamine**
301 **and performance in a reinforcement learning task: evidence from Parkinson's**
302 **disease.** *Brain* 2012, **135:1871-1883.**
- 303 21. Seymour B, Maruyama M, De Martino B: **When is a loss a loss? Excitatory and**
304 **inhibitory processes in loss-related decision-making.** *Current Opinion in*
305 *Behavioral Sciences* 2015, **5:122-127.**
- 306 22. Tom SM, Fox CR, Trepel C, Poldrack RA: **The neural basis of loss aversion in**
307 **decision-making under risk.** *Science* 2007, **315:515-518.**
- 308 23. Jensen J, McIntosh AR, Crawley AP, Mikulis DJ, Remington G, Kapur S: **Direct**
309 **activation of the ventral striatum in anticipation of aversive stimuli.** *Neuron* 2003,
310 **40:1251-1257.**
- 311 24. den Ouden HE, Daw ND, Fernandez G, Elshout JA, Rijpkema M, Hoogman M, Franke
312 B, Cools R: **Dissociable effects of dopamine and serotonin on reversal learning.**
313 *Neuron* 2013, **80:1090-1100.**
- 314 25. Palminteri S, Khamassi M, Joffily M, Coricelli G: **Contextual modulation of value**
315 **signals in reward and punishment learning.** *Nat Commun* 2015, **6:8096.**
- 316 26. Rigoli F, Friston KJ, Dolan RJ: **Neural processes mediating contextual influences on**
317 **human choice behaviour.** *Nat Commun* 2016, **7:12416.**
- 318 27. Chen X, Mohr K, Galea JM: **Predicting explorative motor learning using decision-**
319 **making and motor noise.** *PLoS Comput Biol* 2017, **13:e1005503.**
- 320 28. Reis J, Schambra HM, Cohen LG, Buch ER, Fritsch B, Zarahn E, Celnik PA, Krakauer
321 JW: **Noninvasive cortical stimulation enhances motor skill acquisition over**
322 **multiple days through an effect on consolidation.** *Proc Natl Acad Sci U S A* 2009,
323 **106:1590-1595.**
- 324 29. Diedrichsen J, Kornysheva K: **Motor skill learning between selection and execution.**
325 *Trends Cogn Sci* 2015, **19:227-233.**
- 326 30. Takikawa Y, Kawagoe R, Itoh H, Nakahara H, Hikosaka O: **Modulation of saccadic eye**
327 **movements by predicted reward outcome.** *Exp Brain Res* 2002, **142:284-291.**
- 328 31. Xu-Wilson M, Zee DS, Shadmehr R: **The intrinsic value of visual information affects**
329 **saccade velocities.** *Exp Brain Res* 2009, **196:475-481.**
- 330 32. Reppert TR, Lempert KM, Glimcher PW, Shadmehr R: **Modulation of Saccade Vigor**
331 **during Value-Based Decision Making.** *J Neurosci* 2015, **35:15369-15378.**
- 332 33. Manohar SG, Chong TT, Apps MA, Batla A, Stamelou M, Jarman PR, Bhatia KP, Husain
333 M: **Reward Pays the Cost of Noise Reduction in Motor and Cognitive Control.**
334 *Curr Biol* 2015, **25:1707-1716.**
- 335 34. Sackaloo K, Strouse E, Rice MS: **Degree of Preference and Its Influence on Motor**
336 **Control When Reaching for Most Preferred, Neutrally Preferred, and Least**
337 **Preferred Candy.** *OTJR (Thorofare N J)* 2015, **35:81-88.**
- 338 35. ten Brinke MM, Boele HJ, Spanke JK, Potters JW, Kornysheva K, Wulff P, AC IJ,
339 Koekkoek SK, De Zeeuw CI: **Evolving Models of Pavlovian Conditioning:**
340 **Cerebellar Cortical Dynamics in Awake Behaving Mice.** *Cell Rep* 2015, **13:1977-**
341 **1988.**
- 342 36. Kornysheva K: **Encoding Temporal Features of Skilled Movements-What, Whether**
343 **and How?** *Adv Exp Med Biol* 2016, **957:35-54.**
- 344 37. Williams JM, Krane V: *Applied Sport Psychology: Personal Growth to Peak*
345 *Performance:* McGraw-Hill Education; 2014.
- 346 38. Burton D, Raedeke T: *Sport psychology for coaches.* USA: Human Kinetics; 2008.

- 347 39. Thorndike E: **Some Experiments on Animal Intelligence**. *Science* 1898, **7**:818-824.
- 348 40. Wong AL, Lindquist MA, Haith AM, Krakauer JW: **Explicit knowledge enhances**
- 349 **motor vigor and performance: motivation versus practice in sequence tasks**. *J*
- 350 *Neurophysiol* 2015, **114**:219-232.
- 351 41. Deci EL, Koestner R, Ryan RM: **A meta-analytic review of experiments examining the**
- 352 **effects of extrinsic rewards on intrinsic motivation**. *Psychol Bull* 1999, **125**:627-
- 353 668; discussion 692-700.
- 354 42. Nikooyan AA, Ahmed AA: **Reward feedback accelerates motor learning**. *J*
- 355 *Neurophysiol* 2015, **113**:633-646.
- 356 43. Quattrocchi G, Greenwood R, Rothwell JC, Galea JM, Bestmann S: **Reward and**
- 357 **punishment enhance motor adaptation in stroke**. *J Neurol Neurosurg Psychiatry*
- 358 2017.
- 359 44. Galea JM, Mallia E, Rothwell J, Diedrichsen J: **The dissociable effects of punishment**
- 360 **and reward on motor learning**. *Nat Neurosci* 2015, **18**:597-602.
- 361 45. van der Kooij K, Overvliet KE: **Rewarding imperfect motor performance reduces**
- 362 **adaptive changes**. *Exp Brain Res* 2016, **234**:1441-1450.
- 363 46. Kojima Y, Soetedjo R: **Selective reward affects the rate of saccade adaptation**.
- 364 *Neuroscience* 2017, **355**:113-125.
- 365 47. Steel A, Silson EH, Stagg CJ, Baker CI: **The impact of reward and punishment on**
- 366 **skill learning depends on task demands**. *Sci Rep* 2016, **6**:36056.
- 367 48. Dayan E, Hamann JM, Averbeck BB, Cohen LG: **Brain structural substrates of reward**
- 368 **dependence during behavioral performance**. *J Neurosci* 2014, **34**:16433-16441.
- 369 49. Hamann JM, Dayan E, Hummel FC, Cohen LG: **Baseline frontostriatal-limbic**
- 370 **connectivity predicts reward-based memory formation**. *Hum Brain Mapp* 2014,
- 371 **35**:5921-5931.
- 372 50. Dayan E, Averbeck BB, Richmond BJ, Cohen LG: **Stochastic reinforcement benefits**
- 373 **skill acquisition**. *Learn Mem* 2014, **21**:140-142.
- 374 51. Mazzone P, Hristova A, Krakauer JW: **Why don't we move faster? Parkinson's disease,**
- 375 **movement vigor, and implicit motivation**. *J Neurosci* 2007, **27**:7105-7116.
- 376 52. Manley H, Dayan P, Diedrichsen J: **When money is not enough: awareness, success,**
- 377 **and variability in motor learning**. *PLoS One* 2014, **9**:e86580.

378

379 **Noteworthy papers**

- 380 ****6.** Stanley J, Krakauer JW: **Motor skill depends on knowledge of facts**. *Front Hum*
- 381 *Neurosci* 2013, **7**:503.
- 382 *Highly influential paper indentifying the importance of action selection during skill learning.*
- 383 ****14.** Guitart-Masip M, Huys QJ, Fuentemilla L, Dayan P, Duzel E, Dolan RJ: **Go and no-**
- 384 **go learning in reward and punishment: interactions between affect and effect**.
- 385 *Neuroimage* 2012, **62**:154-166.
- 386 *Important paper revealing the interaction between instrumental learning and Pavlovian*
- 387 *biases during decision-making and reinforcement learning.*
- 388 ***25.** Palminteri S, Khamassi M, Joffily M, Coricelli G: **Contextual modulation of value**
- 389 **signals in reward and punishment learning**. *Nat Commun* 2015, **6**:8096.
- 390 *Interesting study showing the importance of a reference point with regard to how a*
- 391 *punishment is coded in the brain during decision-making.*
- 392 ***29.** Diedrichsen J, Kornysheva K: **Motor skill learning between selection and execution**.
- 393 *Trends Cogn Sci* 2015, **19**:227-233.
- 394 *Significant review of the link between selection and execution during motor skill learning.*

- 395 **33. Manohar SG, Chong TT, Apps MA, Batla A, Stamelou M, Jarman PR, Bhatia KP,
396 Husain M: **Reward Pays the Cost of Noise Reduction in Motor and Cognitive**
397 **Control**. *Curr Biol* 2015, **25**:1707-1716.
398 *An extremely important study revealing dopamine-dependent non-learning reward-based*
399 *shifts in the speed-accuracy trade-off.*
- 400 *41. Deci EL, Koestner R, Ryan RM: **A meta-analytic review of experiments examining**
401 **the effects of extrinsic rewards on intrinsic motivation**. *Psychol Bull* 1999,
402 **125**:627-668; discussion 692-700.
403 *A good review of the effects of extrinsic and intrinsic reward in sports coaching.*
- 404 *47. Steel A, Silson EH, Stagg CJ, Baker CI: **The impact of reward and punishment on**
405 **skill learning depends on task demands**. *Sci Rep* 2016, **6**:36056.
406 *An important paper highlighting the impact of task design on the effects of reward and*
407 *punishment in laboratory-based motor skill learning.*
- 408 *48. Dayan E, Averbeck BB, Richmond BJ, Cohen LG: **Stochastic reinforcement benefits**
409 **skill acquisition**. *Learn Mem* 2014, **21**:140-142.
410 *A noteworthy study revealing that stochastic reward leads to substantial improvements in*
411 *skill learning relative to continuous reward within laboratory-based motor skill learning.*