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Running Head: COMPARISON BETWEEN PRISM AND OTHER ADAPTATION
PARADIGMS

Do prism and other adaptation paradigms really measure the same processes?

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Conflict of Interest

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

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3 **Do prism and other adaptation paradigms really measure the same processes?**

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15 **Abstract**

16 Sensorimotor plasticity allows the nervous system to set up appropriate motor and sensory
17 compensations when individuals face changing demands in a given motor task. A much-
18 debated question in neuroscience research is the identification of processes that encompass
19 this capacity of plasticity. Prism adaptation is the oldest experimental paradigm that has been
20 used to achieve this goal (Helmholtz, 1867). Since 1990's, other paradigms have emerged
21 such as visuomotor rotations or dynamical perturbations (inertial Coriolis forces, velocity-
22 dependent force-field).

23 We compared these paradigms with respect to three specific methodological features:
24 application of the perturbation, after-effects, and generalization. This work aimed to shed
25 light on the following central issue: Do all these paradigms involve similar processes? We
26 used generalization properties—a relevant feature associated with the credit assignment
27 problem—to emphasize the involvement of different processes in “adaptation”
28 paradigms. We therefore classified these processes based on the context specificity of elicited
29 transformations.

30 This review reveals that the processes involved are closely linked to paradigm-related
31 experimental conditions. **Context-independent** processes appear to be favored when errors are
32 attributed to our own sensorimotor performance (prism, Coriolis) whereas **context-**
33 **dependent** processes appear to be mostly mediated by attribution of errors to a specific
34 external interface (visuomotor rotation, force-field). This work encourages researchers to
35 consider the methodological aspects specific to each paradigm for future investigations of
36 sensorimotor plasticity.

37

38 **Key words:** prism, adaptation, learning, generalization, self-attribution.

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40

41 **1. Introduction**

42 Humans are remarkably able to produce a variety of accurate motor behaviors despite
43 constantly changing demands. This capacity includes the ability to modify a known behavior
44 to face new conditions (for example, reaching underwater, through magnifying glasses or
45 under a reduced gravitational field). It also includes the ability to acquire a new motor
46 behavior (for example riding a bicycle). A much-debated question in neurosciences research
47 is to identify the processes that encompass this capacity of plasticity.

48 Recently, several reviews have focused on the classification of these adaptive
49 processes using various terms to describe them, such as sensorimotor learning , motor
50 adaptation (Bastian, 2008; Kitago & Krakauer, 2013; Krakauer & Mazzoni, 2011), motor
51 learning (Bastian, 2008; Kitago & Krakauer, 2013), skill learning (Kitago & Krakauer, 2013;
52 Makino et al., 2016), skill acquisition (Kitago & Krakauer, 2013), sensory perceptual learning
53 (Bedford, 1993; Makino et al., 2016), sensorimotor associative learning (Makino et al., 2016),
54 etc.

55 Despite the use of varying definitions and terms, these reviews share a couple of key
56 features and refer to two main notions: “adaptation” and “learning”. Unfortunately, these
57 terms are often used interchangeably and without precision. However, several attempts of
58 definitions have been proposed. For Bastian (2008), “adaptation” broadly refers to the
59 modification of a pre-existing pattern in response to altered conditions. “Learning” is the
60 acquisition of a new motor program or skill. In addition, Bastian suggests that “adaptation”
61 must imply “after-effects”. This means that participants cannot retrieve their prior behavior
62 once adapted, unless they de-adapt. On the other hand, “learning” is associated with the
63 possibility to store the new movement pattern, so it becomes immediately available in the
64 appropriate context. These characteristics may imply differences concerning the context
65 specificity of elicited transformations. In fact, as an adjustment of the sensorimotor system to
66 new conditions, the consequences of adaptation should apply to different movements
67 performed by the subject. Thus, it would not be limited to the target and conditions that were
68 practiced during exposure to the perturbation, but should extend across space (Bedford, 1993;
69 Redding, Rossetti, & Wallace, 2005; Torres-Oviedo & Bastian, 2012). Conversely, learning
70 would be highly contextual. As such, learning would not extend to other types of action
71 toward the environment or to other experimental conditions, as long as these conditions are
72 completely different from those experienced during the learning session (e.g. learning to

73 smash in tennis should not interfere with the ability of riding a bicycle) (Wolpert & Flanagan,
74 2010). Obviously, adaptation may also be context-dependent and learning a skill such as
75 riding a bicycle is known to generalize to other types of bicycles (Braun, Aertsen, Wolpert, &
76 Mehring, 2009). Thus, the classification between adaptation and learning might be confusing.

77 Generalization properties appear to be particularly interesting and meaningful in order
78 to question the processes involved during adaptation paradigms. In fact, patterns of
79 generalization provide clues about the nature of representational transformations set up by the
80 nervous system to face a given perturbation (Poggio & Bizzi, 2004; Taylor & Ivry, 2013).
81 Additionally, the possibility to transfer compensations acquired to other conditions might be
82 useful in the field of neurorehabilitation. Therapists aim to design strategies that allow
83 patients to reinvest compensations acquired during rehabilitation in other daily life situations.
84 As such, disentangling the processes through their context-dependency should be of great
85 practical interest. Taylor and Ivry (2013) defined the context by the layout of the target
86 locations. More globally, the context could refer to the whole characteristics of the task
87 performed by the subject during behavioral transformations. It therefore comprises
88 environmental characteristics (e.g., layout of the targets locations, apparatus and settings,
89 instructions) but also individual characteristics (e.g. postural configuration, effectors). As
90 such, context-dependent process implies transformations that are specific to the context in
91 which they emerged (i.e. the perturbation/exposure context). Context-independent process
92 entails compensations that are transferable to other conditions, beyond the exposure context.

93 The oldest paradigm used to explore sensorimotor plasticity is the use of prism
94 goggles to laterally shift the visual field (von Helmholtz, 1867). When a subject wearing
95 prisms points quickly to a near object, he/she initially points to the prism-displaced image of
96 the object, experiencing a pointing error. After tens of pointing attempts, the pointing error is
97 gradually reduced close to zero. This experiment simply depicts the short-term plasticity of
98 the central nervous system (CNS), which allows to adapt to changes in the relationships
99 between visual inputs and corresponding motor outputs (for a review, see Redding et al.,
100 2005).

101 Numerous other “adaptation” paradigms have been used to investigate the
102 compensations set up in response to altered conditions. Among them, dynamical perturbations
103 (either contactless Coriolis forces or force-field) and visuomotor rotation paradigms are the
104 most commonly used. In contactless Coriolis force-field experiments, participants are
105 required to perform reaching movements while sitting on a rotating chair (Coello, Orliaguet,

106 & Prablanc, 1996; Lackner & Dizio, 1994; Lackner & DiZio, 2002). In force-field
107 experiments, a manipulandum produces dynamic forces on the hand while subjects are
108 performing reaching movement toward visual targets with this robotic arm (Shadmehr &
109 Mussa-Ivaldi, 1994). In the case of visuomotor rotations, subjects' index finger position is
110 coupled with the position of a cursor on a screen while they are asked to perform reaching
111 movement. The relationship between the hand position and the cursor position is then
112 perturbed by imposing a clockwise or anti-clockwise rotation of the moving hand visual
113 refference (Krakauer, Pine, Ghilardi, & Ghez, 2000; Krakauer, 2009; Prablanc, Tzavaras, &
114 Jeannerod, 1975).

115 In most contact force-field and visuomotor rotation paradigms, a critical feature is the
116 subject's knowledge of a physical interacting interface (the manipulandum and its tactile
117 feedback) between motor planning and endpoint visual representation. Moreover, in
118 visuomotor rotation, the actual feedback is usually not a direct view of the hand position, but
119 a virtual cursor image of the hand displayed on a screen. Conversely, contactless Coriolis
120 force-field or prism paradigms are related to a contactless discrepancy between motor
121 planning and visual refference. Then, feedback is directly perceived.

122 Another methodological question deserves particular consideration concerning contact
123 force-field and visuomotor rotation paradigms: how would the after-effects change if the
124 contact with the manipulandum was suppressed while keeping the same structure of the
125 adapted/learned movement? A few studies have considered this crucial question (Cothros et
126 al, 2006; Kluzik et al., 2008) and concluded that most of the aftereffect, when present,
127 resulted from the adaptation/learning of the interface properties rather than from the
128 adaptation/learning of the subject's own sensorimotor system. By contrast, in prism
129 adaptation, the after-effect's strength is the same when the prisms are removed or are replaced
130 by null deviation sham prisms. In addition, the different paradigms are associated with various
131 generalization properties. This could underlie the contribution of different processes.

132 Comparison of methodological aspects between "adaptation" paradigms may highlight
133 the fact that adaptive processes actually involved are closely linked to the paradigm used.
134 Through a comprehensive comparison between prisms and other adaptation paradigms, the
135 scope of this review is to identify the contributions of context-dependent vs context-
136 independent processes during these experiments. Particularly, we will focus on three
137 methodological points associated with specific behavioural findings: application of the
138 perturbation, conditions in which after-effects are tested, and assessment of generalization

139 properties. We will discuss how these features could emphasize the possibility that different
140 processes are actually involved. To achieve this, we will review the existing modelings of
141 sensorimotor adaptation and the question of credit assignment. We will focus the review to
142 four most-commonly used error-based paradigms that investigate reaching movements:
143 prisms, Coriolis force-field, force-field and visuomotor rotations.

144

145

146 **2. Practical distinctions between adaptation paradigms**

147 **2.1. Application of the perturbation**

148 The different “adaptation” paradigms share several common features and impose an alteration
149 of sensorimotor coordination by perturbing one or several sensory modalities. Thus, all
150 paradigms evoke an error signal from the discrepancy between predicted and actual sensory
151 reafferences, so-called sensory prediction errors. They are known to trigger the error
152 reduction process (Inoue, Uchimura, & Kitazawa, 2016; Popa, Streng, Hewitt, & Ebner, 2016;
153 Shadmehr, Smith, & Krakauer, 2010; Tseng, Diedrichsen, Krakauer, Shadmehr, & Bastian,
154 2007). Noticeably, the type of perturbation determines the sensory modalities altered during
155 exposure and defines the type of error signals generated. In all paradigms, error signals are
156 triggered by an inconsistency between predicted visual reafferences of the moving hand
157 (derived from an efferent copy) and actual visual reafferences. In both prism studies (Held &
158 Hein, 1958; Diedrichsen, Hashambhoy, Rane, & Shadmehr, 2005; Kawato, 1999; Miall &
159 Wolpert, 1996; Shadmehr, Smith, & Krakauer, 2010) and visuomotor paradigms (Krakauer,
160 2009), the proprioceptive consequences are left unchanged. Error signals can also arise from
161 the discrepancy between vision and proprioception of the hand in prism experiments (Craske
162 & Crawshaw, 1974; Redding & Wallace, 1992). In Coriolis force-field (Lackner & Dizio,
163 1994; Lackner & DiZio, 2002; Sarlegna, Malfait, Bringoux, Bourdin, & Vercher, 2010) as
164 well as tactile force-field (Shadmehr & Mussa-Ivaldi, 1994), the error derives from the
165 conflict between the expected and the actual visual reafferences together with the conflict
166 between expected and actual proprioceptive reafferences. Another important signal in force-
167 field experiments refers to the external forces applied by the robot and felt by the subject.
168 Finally, in all paradigms, error signals can also derive from a reaching feedback error, i.e., the
169 simultaneous vision of the target and hand either during movement (Redding & Wallace,

170 1988) and/or at the end of the movement (Harris, 1963; Kitazawa, Kohno, & Uka, 1995;
171 Martin et al., 1996; Welch & Abel, 1970). This type of error signals respectively refers to
172 dynamic (during movement) or static (terminal error) error (Gaveau, Prablanc, Laurent,
173 Rossetti, & Priot, 2014; Gaveau et al., 2018; O'Shea et al., 2014). The different types of
174 perturbation and the movement errors are illustrated in Figure 1.

175

176 Error reduction curves observed in the different paradigms during exposure are closely similar
177 to each other. Subjects initially experience large errors which are rapidly then gradually
178 reduced until performance approximately reaches baselines. It is important to mention the
179 general observation of an asymptotic level of residual error of about 10 to 20% at the end of
180 the disturbance exposure. This residual error shows an incomplete adaptation that cannot be
181 explained by a duration of limited exposure to disturbance, whether for the prism (Spang,
182 Wischhusen, & Fahle, 2017) or for body-centered visual rotation (van der Kooij, Brenner, van
183 Beers, & Smeets, 2015). To explain such a limitation of the error at the end of a few hundreds
184 of trials, the existence of two simultaneous and opposite learning and forgetting processes has
185 been proposed (Shmuelof et al., 2012; Vaswani et al., 2015) whereby the final level of
186 adaptation is determined by a balance between the two processes (van der Kooij et al., 2015).
187 This striking apparent similarity concerning error reduction curves enhances confusion and
188 encourages straightforward comparisons between paradigms, suggesting that processes
189 involved are also similar.

190 However, an important distinction between paradigms is the existence or not of a mechanical
191 and/or visual interface. Lackner and Dizio (2005) compared identical inertial (Coriolis) and
192 mechanical (force-field) perturbations and showed that the presence of a mechanical contact
193 on the reaching arm was a crucial difference between both paradigms. In fact, in force-field
194 experiments, the perturbation is locally applied through the robotic manipulandum.
195 Conversely, Coriolis forces are globally applied without any external contact cue. In
196 visuomotor rotation experiments, subjects generally hold a mouse or a handle in order to
197 reach the target while prismatic lenses induce a lateral shift that deviates the visual
198 representation of the environment without any external contact cue on the reaching arm.

199 Another substantial distinction concerns the visual perception of the reaching arm during
200 exposure. In Coriolis forces and prisms experiments, subjects perceive their moving arm
201 directly (or through glasses for prisms). Such is generally not the case for force-field and

202 visuomotor rotation experiments during which subjects perceive their moving arm through a
203 2D representation (on a computer screen). These distinctions lead to a crucial difference
204 related to the off-body axis or body centered application of the perturbation. Coriolis forces
205 and prisms are body, head and gaze centered perturbations because there is no mechanical
206 contact on the reaching arm and subjects directly perceive it. Conversely, force-field and
207 visuomotor rotation are applied through an off-body centered arbitrary point because of the
208 presence of tactile contact and computer interface.

209 Noticeably, these paradigm-specific considerations are not always systematic. First, a
210 visuomotor rotation can also be head-centered when generated through virtual environments
211 (van der Kooij et al., 2015; van der Kooij, Brenner, van Beers, Schot, & Smeets, 2013; Vetter,
212 Goodbody, & Wolpert, 1999). Similarly to prisms, it provides a contactless shift of the
213 symbolic or more realistic representation of the hand and limb (Vetter et al., 1999; van der
214 Kooij et al., 2015; Arevalo, Bornschlegl, Eberhardt, Ernst, Pawelzik, & Fahle, 2013) and
215 exhibits similar adaptive properties. Moreover, the visuomotor rotation paradigm does not
216 always require the use of an external device. For example, the finger location can be recorded
217 by an Optotrack marker stuck on the finger (e.g. Simani, McGuire, & Sabes, 2007). Second,
218 in the force-field paradigm, the use of a 2D representation is not always required. Full vision
219 of the actual hand is available in some experiments, but they still involve a device or a tool in
220 contact with the endpoint effector. Finally, although prisms can also be considered as an
221 external device, they are not applied on the moving arm. In addition, prisms experiment can
222 be carried out either with or without contact with the head (Gaveau et al., 2014) and still
223 exhibit the same adaptive processes. Thus, the existence of a physical contact as a source of
224 feedback interaction may characterize the process involved to counteract the perturbation.

225

226 The fact that perturbations are applied through an interface or not is related to the attribution
227 of error to a specific external interface (such as a mouse, or manipulandum) or to our own
228 sensori-motor performance (prism, non-contact gravito-inertial field). Indeed, as discussed
229 further, the attribution of error to either our external environment or our own movement may
230 determine the nature of the compensation process.

231

232 This broad difference among types of perturbations may have substantial
233 consequences on the way the CNS sets up compensations to counteract the perturbation. In

234 fact, alterations developed in response to perturbations that use an interface and involve a
235 tactile contact on the reaching arm (force-field, visuomotor rotations) likely remain specific to
236 the context and to the settings of the perturbation (e.g. to the robot device).

237 2.2. After-effects assessment

238 In order to regain baseline accuracy, the nervous system must compensate for a given
239 perturbation by reducing errors during the initial exposure. This is typically quantified by
240 assessing the presence of sustainable compensations once the perturbation has been removed
241 or so-called after-effects (Krakauer, 2009; Redding et al., 2005; Shadmehr et al., 2010). They
242 generally consist in errors in a direction opposite to the initial perturbation and are typically
243 quantified by subtraction from baseline performance.

244 The procedures used to assess after-effects vary to a certain extent depending on the
245 type of paradigm. Some differences concern the explicit (or not) subtraction of the
246 perturbation before assessing after-effects and the remaining presence of apparatus which is
247 similar to the exposure context. The after-effects observed in the different paradigms are
248 illustrated in Figure 1.

249 In the prism paradigm, after-effects are assessed during a distinct phase called post-
250 tests. At the end of the exposure, the prisms are generally explicitly removed (i.e. the goggles
251 are taken off). The subject therefore unexpectedly experiences a pointing error in the opposite
252 direction to that induced by the prisms (Harris, 1963). This aftereffect (called negative
253 aftereffect) persists for several trials. The measures of these after-effects are generally
254 performed without vision of the hand (open-loop) during the entire movement to prevent de-
255 adaptation. As there is no visual feedback of the error between the target and hand, after-
256 effects last from tens to hundred trials with a long time constant.

257 Assessment of after-effects in Coriolis force-field paradigm is relatively similar to
258 prisms experiments. After the exposure period, subjects are asked not to move during tens of
259 seconds once the chair has stopped so that the vestibular system can return back to its resting
260 state and subjects can feel stationary. Then, subjects are required to perform the same
261 movements of pointing (as during exposure) toward the sagittal target. Movement paths
262 deviate in the same direction as the prior chair rotation at constant velocity. After-effects are
263 quantified as dynamic (during movement) and terminal (at the end movement) reaching
264 deviations, compared to performance during baseline trials (Lackner & Dizio, 1994; Lackner
265 & DiZio, 2002; Lefumat et al., 2015).

266 Visuomotor rotations studies use after-effects assessment methods that are comparable
267 to Coriolis and Prisms experiments. After exposure to the visuomotor rotation, participants
268 perform “probe trials” in order to measure after-effects (Mazzoni & Krakauer, 2006).
269 Reaching movements are performed in the same way as during exposure except that the
270 relationship between hand movement and cursor location is no longer perturbed. Probe trials
271 are performed without visual feedback (“blank trials”) and compared to blank trials measured
272 during baseline, in order to quantify the amount of adaptation. These post-tests trials are
273 sometimes interspersed by “re-learning” trials, during which perturbation is turned on again
274 (Zhou, Fitzgerald, Colucci-Chang, Murthy, & Joiner, 2017). The main difference with the
275 precedent paradigms is that subjects are not explicitly aware of the presence or absence of the
276 perturbation.

277 Assessments of after-effects in force-field paradigms are considerably different than in
278 other paradigms. Once exposure trials lead to an approximate compensation of the force-field,
279 the perturbation is suddenly removed on selected trials, i.e. the forces applied to the
280 manipulandum are turned off. Thus, the movement path is deviated to the opposite direction
281 relatively to initial errors. These selected attempts are called “catch trials” and allow a
282 measure of the immediate aftereffect by quantifying lateral forces applied on the
283 manipulandum. In fact, lateral forces could reflect adaptive compensations of expected lateral
284 forces imposed by the robot (Goodbody & Wolpert, 1998; Shadmehr & Moussavi, 2000;
285 Shadmehr & Mussa-Ivaldi, 1994). However, whereas the hand (or target) feedback loop can
286 be opened in the prism or in the visuomotor rotation paradigm, such is not the case for force
287 feedback as subjects feel the force offset. This makes difficult to compare the open loop decay
288 of the after-effects and those of the other adaptation paradigms. A possibility to reduce error
289 feedback availability (at least visual feedback) is to use “error-clamp” trials. As for catch-
290 trials, force-field is removed on selected trials. In addition, instead of leaving subjects moving
291 the manipulandum in a free way to reach the target, they are kept from experiencing lateral
292 errors. More precisely, movement path is constrained by novel forces to remain strictly
293 straight toward the target. However, the manipulandum still records the lateral forces applied
294 by the subjects (Smith, Ghazizadeh, & Shadmehr, 2006). The crucial point is not only that the
295 perturbation is not explicitly removed but also that after-effects are assessed on exactly the
296 same apparatus than during exposure, i.e. subjects are still holding the manipulandum.
297 Altogether, these differences lead to a difficult comparison between adaptation paradigms
298 because after-effects do not refer to the same probes of adaptation.

299 Nevertheless, some authors have investigated whether after-effects were present
300 following force-field adaptation in changing apparatus settings. Kluzik et al. (2008) tested
301 whether adaptation of reaching movements to a viscous force-field while holding a robotic
302 arm generalized to other conditions. In the robot-null condition, the manipulandum was still
303 attached to the robot but the forces were turned off. In the free-space condition, the
304 manipulandum was explicitly dissociated from the robot. In both conditions, generalization
305 was assessed while participants were still holding the manipulandum. Authors observed that
306 compensatory movements generalized to the free space condition. It is noteworthy that
307 although the term generalization has been used, this procedure rather converges with after-
308 effects measurement in other paradigms. Moreover, although participants were aware that the
309 perturbation was turned off (robot-null condition) and even when the manipulandum was
310 detached from the robot (free-space condition), after-effects were still assessed on the setting
311 in which participants experienced the force-field, i.e. when holding the manipulandum. It
312 cannot be determined if alterations of the visuomotor coordination acquired during adaptation
313 would generalize in situations in which holding the manipulandum is not required. To test for
314 this condition, Cothros and colleagues (2006) investigated the transfer of compensations in a
315 real free-space: participants were not holding the robotic arm at all. They found that after-
316 effects were substantially reduced in the free-space condition. This real-free space condition is
317 more comparable with the procedures used to assess after-effects in prism literature for
318 example. These results confirm the fact that force field training favours the implication of
319 processes that seem to be context dependent.

320 In sum, it is important to attentively consider the conditions in which after-effects are
321 assessed in each paradigm. More precisely, the fact that after-effects are measured on the
322 same apparatus as during the exposure yields to measure potential cognitive components of
323 after-effects specifically related to the training context. As a consequence, different methods
324 to assess after-effects may not reflect the presence of the same processes to counteract the
325 perturbation.

326 **2.3. Generalization properties**

327 Another way to verify that robust adaptive changes have arisen during exposure is to
328 investigate if compensations are persistent and can be observed in different contexts (i.e.
329 conditions different than exposure conditions), a phenomenon named as generalization
330 (Bastian, 2008; Censor, 2013; Poggio & Bizzi, 2004). Similarly to the notion of after-effects,

331 generalization varies among the different paradigms, essentially in terms of definition and
332 assessment methods.

333 First and foremost, the barrier between the notions of after-effects and generalization
334 may be substantially confusing among the different paradigms. For example, measurement of
335 after-effects in a robot-null conditions (force-field turned off) was considered as a measure of
336 generalization in Kluzik et al. previous work (2008) whereas it simply converges to a measure
337 of after-effects with the perturbation removed (closely to prisms experiments). Another
338 important point is that generalization is characterized by a polysemous nature. In fact
339 generalization can constitute a measure of how compensations can be applied in other settings
340 (post-adaptation generalization). Otherwise, trial-by-trial generalization can reflect how the
341 errors experienced on a given trial during exposure can be transferred in other settings under
342 the same perturbation (Tanaka, Krakauer, & Sejnowski, 2012). As we are interested in
343 generalization as a probe that robust changes have emerged in the nervous system during
344 exposure, we limit our analysis to post-adaptation generalization features.

345 In addition, generalization must not be mistaken with another behavioural
346 phenomenon, known as savings. When individuals are re-exposed to the same perturbation,
347 they show faster error reduction process (Huang & Shadmehr, 2009; Kojima, 2004; J. W.
348 Krakauer, 2005; Seidler, Gluskin, & Greeley, 2017; Zarah, Weston, Liang, Mazzoni, &
349 Krakauer, 2008). Recent studies report that these sensorimotor savings are due to recall from
350 visuospatial working memory of early strategic components of adaptation (Morehead, Qasim,
351 Crossley, & Ivry, 2015). In fact, savings can appear after a prolonged period of washout
352 (Krakauer, 2005; Zarah et al., 2008) and seem to appear only when large perturbations are
353 exposed to participants (Morehead et al., 2015). Savings are related to the recall of the
354 initially successful strategy. As such, they are strongly context-dependent and do not reflect
355 the same processes as generalization properties.

356 To clarify the notion of generalization and to facilitate comparison, we consider that
357 generalization refers to a change in assessment context compared to exposure context. This
358 change can be related to unpractised targets or workspace (spatial generalization), other
359 effectors (e.g. interlimb transfer), changing features of tasks (e.g. different speeds) or even
360 other tasks (e.g. wheelchair driving).

361 *Spatial generalization*

362 Spatial generalization has been extensively studied across “adaptation” paradigms.
363 Generalization patterns can be reflected by a monotonous function, with a decrease of transfer
364 as untrained target are pulled away from the trained target (Gharamani et al., 1996).
365 Conversely, transfer of compensations toward locations far from the trained ones has also
366 been reported in prism adaptation as nearly complete (Bedford, 1993).

367 Distinct results are found across paradigms. For example, some studies in prism literature
368 allowed to draw a slight gradient of decay as one moves away from the area explored during
369 the exposure (Gogel & Tietz, 1974).

370 Similarly, some components of after-effects following prisms exposure have been shown to
371 transfer across non-learned locations as long as the exposure spatial maps were also involved
372 during post-exposure testing. However, others components generalized associatively with
373 respect to similarity between conditions during exposure and post-exposure, i.e. associative
374 generalization (Redding & Wallace, 2006). These context-dependent after-effects were
375 related to a kind of cognitive learning and highlighted the different processes involved in
376 responses to prismatic perturbations (see next section for details) (Bedford, 1993, 1999). In
377 the prism literature, the spatial generalization of after-effects is measured when the
378 perturbation is explicitly removed.

379 On the other hand, force-field experiments have also broadly studied spatial
380 generalization and mainly report a generalization to a limited range of adjacent directions. An
381 important point is that generalization does not always refer to the transfer of after-effects but
382 often to the transfer of “adaptation”. In the latter, generalization is tested toward other
383 locations but under the same force-field perturbation (Goodbody & Wolpert, 1998). As such,
384 this type of measure reflects a trial-by-trial generalization and does not probe the presence of
385 robust and transferable compensations acquired in response to the perturbation. In others
386 studies, spatial generalization was assessed using catch trials (i.e. force-field turned off):
387 transfer was present for neighbouring targets but decayed quickly when distance from the
388 trained targets increased (Donchin, Francis, & Shadmehr, 2003; Gandolfo, Mussa-Ivaldi, &
389 Bizzi, 1996; Mattar & Ostry, 2007).

390 A limited spatial generalization is also present in visuomotor rotation experiments. In
391 fact, a narrow spatial tuning is observed, with a sharp gradient around the trained direction
392 highlighting a poor generalization across multiple directions. For example, after training in a
393 single direction, after-effects dropped off by a very large ratio when aiming at 45 degrees
394 apart from the learned location (Ghahramani, Wolpert, & Jordan, 1996; Pine, Krakauer,

395 Gordon, & Ghez, 1996). Krakauer et al. (2000) showed that adaptation of gain (distance) to
396 visuomotor rotations generalized to untrained gains while adaptation of rotation (direction)
397 did not. However, tests of generalization were conducted under the same perturbation as
398 during exposure. Vetter et al. (1999) conducted tests of generalization under a virtual
399 environment that simulated a terminal feedback prism displacement. They found post-
400 adaptation generalization toward the entire workspace. However, these post-exposure trials
401 were interspersed every 3 trials by perturbed trials to prevent decay of learning.

402 *Interlimb transfer*

403 Concerning transfer to untrained effectors, several authors in prism studies have highlighted
404 the existence of transfer to the unexposed arm (Choe & Welch, 1974; Taub & Golberg, 1973).
405 Conversely, Prablanc et al. (1975) reported that two arms can be adapted to opposite prism
406 displacement which was replicated in monkeys (Yin & Kitazawa, 2001) and suggested a null
407 or weak inter-manual transfer. A limited inter-manual transfer of prism adaptation was
408 however observed when the exposure involved pointing movements crossing the body
409 midline, in the contralateral field to the exposed arm (Prablanc et al 1975b). The transfer was
410 possibly explained by a trunk rotation.

411 Most of the other studies which found inter-manual transfer of prism adaptation did not
412 investigate visual aftereffects derived from visuo-oculomotor adaptation which generalize to
413 both hands nor did they measure a possible neck proprioceptive after-effect. Inter-manual
414 transfer has been reported with unconstrained head movement during exposure (Hamilton,
415 1964). As this condition produces a change in the felt head position (Redding & Wallace,
416 2003, 2004), it obeys the axio-proximo-distal hierarchy (eye-head-neck-arms) such that the
417 inter-manual transfer appears to be a sub-product of axial adaptive sensory representations.

418 Norris et al. (2001) investigated the reciprocal transfer of prism displaced vision between
419 either the real hand or more abstract representations of the hand – online video view of the
420 hand or online view of a cursor representing the hand. The cursor exposure condition elicited
421 very small after-effects during real hand pointing, whereas prism displaced vision of the own
422 hand elicited a full transfer of after-effects to hand pointing with the cursor. A possible
423 explanation is that direct view of the hand when the prism angle is moderate does not alter the
424 sense of ownership and does not call for unnatural representations, which is further discussed
425 in the last part of the paper.

426 Finally, Renault et al. (2018) reported inter-manual transfer following prism exposure that
427 could be either intrinsic or extrinsic, illustrating the complexity and the large range associated
428 with this kind of transfer.

429 The transfer across limbs (inter-manual transfer) is the only aspect of generalization
430 that has been explored in Coriolis force-field paradigm. For example, Lefumat and colleagues
431 (2015) have reported a limited but significant interlimb transfer following a Coriolis force-
432 field adaptation. Moreover, they showed that individual characteristics (notably, motor
433 variability during late adaptation phase and laterality quotient) had a positive influence on
434 interlimb transfer.

435 Patterns of interlimb transfer in force-field experiments suggest a transfer from the
436 dominant arm to the non-dominant arm (Criscimagna-Hemminger, Donchin, Gazzaniga, &
437 Shadmehr, 2003). In that study, transfer was assessed by interspersed catch trials during
438 exposure to the field. As for visuomotor rotation, Wang and Sainburg (2004) showed that
439 training under a visuomotor rotation with one limb facilitated the subsequent learning of the
440 same rotation with the other limb while other authors reported a limited interlimb transfer
441 (Krakauer et al., 2000). Additionally, Imamizu and Shimojo (1995) showed a nearly complete
442 inter-manual transfer of adaptation which was carried out with a 90 degrees visual rotation.
443 This is possibly related to a rule learning at task level rather than an adaptation process at
444 muscle level. Krakauer et al (2006) also observed that visuomotor rotation adaptation
445 transferred from the arm to the wrist, but not vice versa, in agreement with a proximo-distal
446 hierarchy of adaptation

447

448 In each paradigm, divergent results are drawn but it appears that a substantial interlimb
449 transfer (mostly from dominant arm to non-dominant arm) does exist. It suggests that
450 compensations acquired from one limb are available for other limbs. However, this kind of
451 transfer might emerge from a cognitive component as a general rule integrated by the nervous
452 system and applicable to other effectors (Malfait & Ostry, 2004; Wang & Sainburg, 2004).
453 Thus, except when it is related to oculomotor or head-neck sensorimotor changes, interlimb
454 transfer relies upon an arbitrary high-level transformation which may reveal changes different
455 from modifications reflected by spatial generalization and transfer to other tasks.

456 *Transfer to other tasks*

457 The term generalization has also been used to describe the transfer of prismatic
458 adaptation to movements different from those used during exposure (Harris, 1965). However,
459 the amplitude of prism adaptation decreased when the post-exposure task differed from that of
460 adaptation (Harris, 1965). Martin et al. (1996) have clarified the limits of these
461 generalizations by restricting them to motor synergies and by showing that an adaptation of
462 dart throwing through prisms obtained in a given postural configuration of the upper limb did
463 not generalize to a throw in the symmetrical postural configuration (i.e. throwing over the
464 shoulder vs throwing from below the shoulder). This suggests a specific adaptation of muscle
465 synergies.

466 Moreover, a specificity of the temporal components of adaptation has been
467 demonstrated by Kitazawa et al. (1997). The rate of adaptation seemed to very specifically
468 depend on the motor pattern used during exposure. The movements performed at the same
469 speed as those performed during the exposure exhibited the highest degree of adaptation,
470 whereas movements at different speeds showed a lower degree of adaptation. In addition, the
471 amplitude of the after-effect decreased when the post-exposure task differed from exposure
472 task (Baraduc & Wolpert, 2002) which suggests that adaptation is dependent on postural
473 configuration.

474 By contrast, after-effects following prism adaptation appeared to generalize to other
475 types of tasks, such as goal oriented walking task (Michel, Vernet, Courtine, Ballay, & Pozzo,
476 2008) or wheel-chair driving (Jacquin-Courtois, Rode, Pisella, Boisson, & Rossetti, 2008;
477 Watanabe & Amimoto, 2010). In addition, a generalization to sensory modalities unexposed
478 to the conflict, such as a target acoustic target, has been identified (Harris, 1963; Craske,
479 1966, Lackner, 1974). This effect suggests a modification of the supra-modal perception of
480 space of an axial reference frame, which likely corresponds to a change in body
481 representations. Moreover, some authors reported expansion of after-effects to higher level
482 cognitive functions (for a review, see Jacquin-Courtois et al., 2013). Such is apparently not
483 the case for other paradigms, notably force-field (Michel, Bonnetain, Amouro, & White,
484 2018).

485 Generalization to other types of tasks has been sparsely studied using other paradigms. In
486 force-field experiments, Conditt et al. (1997) have suggested that compensations acquired to
487 counteract a given force-field generalized from straight movements to circular movements
488 (either post and trial-by-trial generalization).

489

490 In sum, the comparison between methods of assessing after-effects and generalization
491 in adaptation paradigms reveals broad dissimilarities associated with various behavioral
492 findings. These dissimilarities are reported in Table 1.

493 Conditions in which after-effects are assessed in the different paradigms have a crucial
494 impact on the interpretation of underlying processes. Comparing findings about these features
495 between paradigms irrespectively of specific conditions and contexts can lead to specious
496 conclusions. In fact, assessing after-effects on the same apparatus and when the perturbation
497 is not explicitly removed (for typical example: catch trials or error clamp trials during force-
498 field experiments) may rather reflect retention, which refers to the capacity of the nervous
499 system to fully or partially maintain the adapted state (Inoue et al., 2015). The conditions in
500 which after-effects are measured are a crucial aspect of what is really assessed. Moreover, it is
501 noteworthy that error reduction during exposure is generally almost complete (i.e. subjects
502 regains near-baseline performance and thus substantially compensate the perturbation) while
503 the amount of after-effects is not equivalent to the amount of the perturbation (Redding &
504 Wallace, 1993). This suggests that mechanisms other than “true adaptation” (Redding and
505 Wallace, 2002) contribute to the reduction of error during exposure. Thus, adaptation must be
506 identified by the presence of robust and context-independent after-effects (Redding et al.,
507 2005). Indeed, a reduction of errors without after-effect implies that the compensation has
508 been achieved through strategic rather than adaptive mechanisms (Kluzik et al., 2008).

509

510 It is neither straightforward to compare generalization properties as they highly depend
511 on the procedures used to measure them, and even more on the conditions set up during
512 exposure. These differences may reflect the fact that different processes are involved
513 depending on the type of perturbation used. Robust generalization of after-effects (i.e. outside
514 the exposure apparatus) likely reflects an adaptive process which is context independent (e.g.
515 spatial generalization in prisms (Bedford, 1989)). Conversely, the absence of generalization to
516 other conditions is associated with a high contribution of context-dependent processes
517 (Cothros et al., 2006; Mattar & Ostry, 2007). It is noteworthy that interlimb transfer is a
518 particular aspect of transfer to other conditions as it could imply higher representations and
519 may not reflect the involvement of context independent processes.

520 Considering these dissimilarities, it is probable that different mechanisms are actually
521 involved according to the paradigm that generalization features may allow to distinguish.

522

523 **3. From paradigms specificity to involved processes: the role of context-** 524 **dependency**

525

526 So far, we have described three specific methodological differences between
527 adaptation paradigms: application of the perturbation, assessment of after-effects, and
528 generalization properties. The highlighted differences reflect the involvement of different
529 processes in adaptation paradigms. In the next section, we will discuss the distinction between
530 context-dependent vs context-independent processes with respect to the theoretical modeling
531 of adaptation processes. Particularly, we will question the frame of internal representations
532 and model-based vs model-free processes. Then, we will discuss how the credit assignment
533 problem can be related to the context-dependency of involved processes.

534 **3.1. Internal representations: model-based vs model-free processes**

535 In order to generate an appropriate movement, our nervous system is able to rely on
536 available information to produce estimates about our own body's state as well as external
537 world. These information arise from internal models that can be specified into several
538 categories. Schematically, the inverse model allows to transform a desired behavioral goal
539 into an appropriate motor commands to achieve it (Miall & Wolpert, 1996; Wolpert,
540 Ghahramani, & Jordan, 1995). Working on the opposite direction, the forward model refers to
541 our ability to predict the consequences of our motor commands. Its output is the predicted
542 reafferences and depends mainly on the previous representation of our own body and
543 secondarily of the environment. When our brain generates a motor command, the forward
544 model receives a copy of this motor command (named as efference copy) and is able to
545 develop predictions about the sensory consequences of the upcoming action, even when the
546 actual sensory reafferences are absent at movement onset. Thus, the forward model can be
547 used to make fast movement corrections prior to and in the early phase of movement
548 execution. Predicted consequences are then compared with the actual consequences of the
549 action, and both are integrated together to get optimized estimates of the world and of the
550 body interactions. The discrepancy between actual and predicted reafferences, called the
551 "prediction error", acts as a signal error signal that triggers adaptive processes to maintain
552 accuracy of both inverse and forward models. Combined inverse and forward models

553 theoretically allow the CNS to carry out a desired action such as arm reaching and to
554 accurately control the unfolding of the reach (Kawato, 1999).

555

556 However, these forward models are useless if they are not accurate enough. The discrepancy
557 between actual and predicted reafferences, called the “prediction error”, acts as a signal error
558 signal that triggers adaptive processes to maintain accuracy of both inverse and forward
559 models.

560 The role of sensory prediction errors as a trigger of adaptation has been suggested in
561 many studies using different paradigms (Bastian, 2006; Diedrichsen et al., 2005; Held, 1961;
562 Taylor & Ivry, 2012; Tseng et al., 2007). Using prism deviation, actual visual reafferences are
563 biased and no longer match the predicted visual consequences. Similarly, visual reafferences
564 of motor commands are also perturbed during visuomotor rotations. Although prism and
565 rotated feedback paradigms both imply the same type of visual mismatch between expected
566 and actual reafferences, they fundamentally differ by the nature of the reafferences (real
567 versus symbolic, and body-centered versus off body-centered). Concerning Coriolis force and
568 force-field paradigms, both types of visual and proprioceptive reafferences are similarly
569 altered, but they fundamentally differ by the nature of the kinesthetic reafferences (internal
570 versus external tactile forces, and body-centered versus off body-centered)

571 The necessary adjustment of internal models to counteract the perturbation is triggered by
572 these different sensory prediction errors. The fact that perturbations are applied either through
573 an interface or without may lead to important implications for the type of internal models that
574 are adjusted. The sensory cues associated with grasping an object (e.g. the robotic
575 manipulandum in force-fields) may promote the development of a distinct internal model
576 associated with this specific object rather than internal model referring to the limb (Cothros et
577 al., 2006). As a consequence, different types of perturbation may not involve the same
578 processes. Adjustment of a distinct interactive model associated with an object may rely on a
579 context-dependent process because this adjustment would be specific to the object.

580 Conversely, adjustment of internal model of the subject alone would imply sustainable
581 transformations in other conditions, i.e. a context-independent process. Another internal
582 source of adaptation results from the realignment of vision and proprioception, which can be
583 achieved by modifications of the visual and/or proprioceptive systems (Kornheiser, 1976).

584 Proprioception and prediction are difficult to disentangle as none can be experimentally

585 removed, as opposite to vision. This is especially clear for prism adaptation, as the prisms
586 only deviate the seen and not the felt location of the hand. It therefore involves a perceptual
587 remapping, such as a change in the straight-ahead visual perception related to a bias in the
588 straight-ahead eye position toward the deviated visual field (Craske, 1967). This perceptual
589 remapping can also concern proprioception of the exposed limb (Harris, 1963) in the direction
590 opposite to the deviated visual field. Such can also be the case in the visuomotor rotation
591 paradigm which also seems to rely on both sensory and motor rearrangements despite the
592 dissimilarities with prism paradigm (Cressman and Henriques, 2009, 2010; Cressman,
593 Salomonczyk, & Henriques, 2010; Clayton, Cressman, & Henriques, 2014). Either of these
594 perceptual adaptations corresponds to a shift of the typically spatially congruent relationship
595 between the visual and the proprioceptive maps of the body parts.

596

597

598 Among the different paradigms, several models of the processes involved during
599 adaptation have been proposed. Some studies suggest that adaptation is driven by multiple
600 systems that learn and forget at different timescales (Huberdeau, Krakauer, & Haith, 2015;
601 Smith et al., 2006; K. van der Kooij et al., 2013). Most of the time, two possible timescales
602 are proposed (two-state model). A fast process would account for rapid correction of
603 movement errors during early adaptation but would be associated with a poor retention (i.e.
604 little after-effects). In a second phase, a slow process would operate and lead to a stronger
605 retention once the perturbation is removed. In other words, error reduction in the very first
606 trials during exposure is mostly accounted for by the fast system that saturates rapidly, while
607 the slow system takes place more gradually during late exposure trials. Moreover, the
608 contribution of the slow system is related to the amount of long-term retention (Yin and
609 Kitazawa, 2001; Joiner & Smith, 2008) as well as to the amplitude of after-effects during
610 prism adaptation (Inoue et al., 2015).

611 Along with this timescale distinction, several authors have proposed to differentiate between
612 implicit and explicit processes. An explicit cognitive strategy is thought to drive the fast
613 correction of movement errors during early adaptation while implicit process contributes
614 mainly to the presence of after-effects. The implicit process can be based on prediction error
615 (Mazzoni & Krakauer, 2006; Taylor & Ivry, 2012; Taylor, Krakauer, & Ivry, 2014) or on
616 visuo-proprioceptive conflict (Redding et al., 2005)

617 The two-state model has been proposed for each type of perturbations: force-field
618 (Albert & Shadmehr, 2018; McDougle, Bond, & Taylor, 2015; Smith et al., 2006),
619 visuomotor rotations (Mazzoni & Krakauer, 2006; Taylor et al., 2014) and prism literature
620 (Petitet, O'Reilly, & O'Shea, 2017; Redding et al., 2005; Redding & Wallace, 2002).
621 'Strategic recalibration' refers to the fast process and allows the fast reduction of movement
622 errors at the beginning of the exposure. Typically, when the subjects miss the target, they
623 would more or less consciously aim at the side of the target on the next trial in order to reduce
624 the previous motor error. Nevertheless, this process is associated with a poor contribution to
625 after-effects. In contrast, 'spatial realignment' in prism adaptation refers to the slow process
626 and contributes mainly to the presence of after-effects. It consists of the reduction of the
627 mismatch between two sensorimotor coordinate systems: an eye-head visual motor system
628 and a head-hand proprioceptive motor system (Redding et al., 2005; Redding & Wallace,
629 2002). The prismatic deviation induces a discordance between these two sources of
630 information. Realignment requires the adjustment of this relationship in order to counteract
631 the perturbation. Strategic compensation and true adaptation are not always easy to tease
632 apart. O'Shea et al. (2014) observed that each type of compensation could be quantified
633 through the analysis of kinematic patterns change during prism exposure. Inoue et al. (2014)
634 suggested the presence of a third timescale in prism adaptation, named as an "ultraslow"
635 process. They showed that a two-state model was not sufficient to explain behavioral data
636 from 150 to 500 exposure trials. However, a three-state model comprising an ultraslow
637 process fits better the data obtained for 500 trials. Moreover, the amount of adaptation in this
638 ultraslow process was strongly correlated with the amount of long-term retention (tested 24
639 hours after the adaptation). Finally, authors suggested that this three-state model can also
640 explain data from experiments in force-field paradigms.

641 These two-state models are defined as model-based processes because they rely on
642 adjustments to internal models that are driven by sensory prediction errors. More specifically,
643 only the slow component of the two-state model may be referred as a model-based process.
644 The fast strategic process would thus be categorized as a "model free" process. Interestingly,
645 Huang and colleagues (2011) have proposed two additional learning processes during
646 adaptation paradigm (visuomotor rotations): operant reinforcement and use-dependent
647 learning. They have suggested that these processes are model-free as they are associated with
648 a memory for action independently of an internal model and are driven directly by task
649 success. Thus, pure adaptation itself would lead to a bias toward the repeated direction of

650 hand space, a process named as use-dependent learning. The presence of use-dependent
651 learning was also probed in force-field experiment (Diedrichsen, White, Newman, & Lally,
652 2010). Moreover, operant reinforcement may also be at work during “adaptation”
653 experiments. Movement results (i.e. success or relative success) act as implicit rewards that
654 lead to the association between successful error reduction and the motor commands
655 converged upon by adaptation (van der Kooij et al., 2018; Huang et al., 2011; Krakauer &
656 Mazzoni, 2011). According to the authors, model-based and model-free processes are not
657 competitive but operate cooperatively during so-called “adaptation” paradigms. Krakauer and
658 Mazzoni situated use-dependent learning and operant reinforcement in the middle of an
659 adaptation to learning continuum. However, although these processes appear to be at work
660 during force-field and visuomotor rotation experiments, it is still unknown if they are implied
661 during prism and Coriolis force-field experiments.

662 Along with the adaptation-to-learning continuum, some authors coined the term of
663 structural learning (Braun et al., 2009; Genewein, Hez, Razzaghpanah, & Braun, 2015). When
664 subjects are exposed to randomly varying tasks of the same structure (visuomotor rotations),
665 authors suggested that subjects are able to extract the structure of the task. As a consequence,
666 when exposed to another task with the same structure, they exhibit learning facilitation. In
667 other words, individuals extract general rules about a class of behaviors, a process so-called
668 structural learning.

669 The presence of multiple adaptive processes during these types of experiments is strongly
670 recognized, and the distinction of model-free vs model-based processes is of growing
671 evidence. However, the relative weighting of both processes may differ between the different
672 “adaptation” paradigms. In addition, although model-based processes are likely related to
673 context-independent processes, it is still unclear to what extent model-free processes can be
674 classified as being context-dependent or context-independent. As they are placed on a
675 learning-to-adaptation continuum, these processes are likely situated between context-
676 dependent and context-independent processes.

677

678 *3.2.Credit assignment: self-attribution of errors as a trigger of context independent* 679 *processes*

680 The role of sensory prediction errors driving the slow process of the two-state model
681 can explain adaptive processes in non-contact Coriolis force and prism paradigm on one side

682 and force-field and feedback rotation on the other side. Thus, the involved processes could
683 appear as very similar. However, as we have highlighted thus far, the observed patterns of
684 generalization are paradigm-dependent. For example, in force-field experiment, authors report
685 very few transfer of compensations to free-space and natural hand movements (Cothros et al.,
686 2006; Kluzik et al., 2008) suggesting that the properties of the tool has been learnt without or
687 with little change in the properties of the effector. These dissimilarities cast some doubt on the
688 universality of the processes really involved to cope with the different types of perturbations.

689 It has been suggested that adaptation processes are related to solving a credit assignment
690 problem (Wilke, Synofzik, & Lindner, 2013). In fact, there are plenty of potential factors for a
691 given movement error. The nervous system is able to assign to an external or to an internal
692 cause the occurrence of errors. For example, error in movement can arise from a perturbation
693 imposed by the environment that explicitly refers to external causes. Another potential source
694 can be muscular fatigue which is an internal cause that refers to our own body. The attribution
695 of errors to extrinsic versus intrinsic coordinates may be associated with differences in the
696 degree of generalization. For example, Berniker and Kording (2008) suggested that if errors
697 are assigned to a change in limb properties (internal cause), generalization appears across the
698 workspace but not across movement with the other limb. In addition, it has been suggested in
699 a rotation paradigm that the “recalibration” of internal sensory predictions (i.e. update of
700 forward internal model to face perturbation) was closely depending on the attribution of
701 predictions errors to internal causes (Wilke et al., 2013).

702 In a coherent manner, the awareness of the perturbation is also closely related to the
703 credit assignment problem. When a subject consciously perceives the perturbation, the
704 observed error is believed to be the result of either a change in the external environment or a
705 misrepresentation of the action. It is therefore logical that adaptation, or learning, becomes
706 strongly associated with the context in which it is elicited. The adjustment is then a local
707 rearrangement tied to a particular situation in which the CNS learns a new visuomotor
708 transformation with a narrow spatial (Krakauer & Mazzoni, 2011) or velocity (Kitazawa et
709 al., 1997) adjustment. However, when the subject is not aware of the perturbation, (e.g.
710 introduced gradually), the CNS can interpret errors as a result of its own variability, and thus
711 correct some of the basic coordination parameters that underlie the organization of the
712 sensorimotor system. A consistent probe of this idea is that gradually introduced perturbations
713 are associated with stronger after-effects (Malfait & Ostry, 2004; Magescas & Prablanc 2006;
714 Michel, Pisella, Prablanc, Rode, & Rossetti, 2007). Under small or moderate systematic

715 perturbations (lower than 12 degrees), when the real hand and forelimb are seen, self-
716 attribution of the error is obviously straightforward.

717 Consistently, Wei and Kording (2009) pointed out that adaptation is strongly related to
718 the relevance of perceived movement errors. In other words, the nervous system would not
719 successfully adapt if perceived errors are judged as irrelevant. Errors that are long lasting, not
720 consciously perceived and/or attributed to the internal causes are more likely categorized as
721 relevant errors, i.e. errors that need the adjustment of inverse and forward models to be
722 corrected. Therefore, this type of error attribution would favor the implication of context-
723 independent processes that allow generalization of compensations.

724 Therefore, a likely functional hypothesis would be that when errors are assigned to an
725 external cause, compensations counteracting the perturbation would be local and contextual
726 and thus would not or little generalize towards other conditions. Conversely, if errors are
727 assigned to an internal cause, perturbation would lead to the generalization of compensations
728 to other conditions. Thus, true adaptation would occur when new mappings of internal
729 representations about our own body are generated to counteract the perturbation, and mainly
730 when perturbation is assigned to internal causes. On the contrary, if the perturbation
731 encountered is assigned to an external cause, the nervous system would modify internal
732 representations about the environment and the self, restricted to the particular context in
733 which perturbations were produced. For this reason, compensations might not transfer to
734 conditions different than those experienced during perturbation. Additionally, exposure
735 context would directly influence the solving of credit assignment problem and therefore the
736 processes involved. This possible explanation can support the main difference observed
737 between body/head centered perturbations versus perturbation off- body/head centered using
738 an interface/tool. That may explain the differences in generalization across paradigms and
739 therefore suggests that different adaptive processes are actually involved. For example, in
740 force-field experiment, the compensations that are considered as adaptation may in fact be
741 mostly related to the establishment of specific new mappings when using the interface
742 because movement errors are assigned to an external cause. Thus, the processes involved may
743 imply compensations associated with a strong context specificity i.e., context-dependent
744 processes.

745

746 **4. Discussion and Conclusion**

747 The aim of this paper was to compare methodologies used to investigate sensorimotor
748 plasticity processes. We focused on methods described as “adaptation” paradigms: Coriolis
749 forces, force-field, visuomotor rotation and prismatic lenses. We compared those paradigms
750 with respect to three specific methodological features (application of the perturbation, after-
751 effects assessment and generalization properties). The purpose of this work was to shed light
752 on this central issue: Do all these paradigms exhibit similar processes and or do they involve
753 distinct functional processes? To answer this question, we used generalization properties as a
754 relevant feature associated with credit assignment problem to emphasize the involvement of
755 different processes in “adaptation” paradigms. We attempted to reveal the link between
756 generalization properties and context-dependency entailed by experimental conditions.

757 Similarities are present between the different paradigms. Similar error reduction
758 curves (rapid then gradual decrease of errors) and the presence of “after-effects” (opposite to
759 the direction of the initial perturbation) are observed across all paradigms. Nevertheless,
760 important differences can be seen between the different methods in particular concerning the
761 application of the perturbation (contact vs contactless perturbation; body-centered vs off
762 body-centered). Another important dissimilarity is how the after-effects and generalization are
763 assessed (removal vs remaining presence of the perturbation settings), highlighting a lack of
764 consensus on these concepts across paradigms. Given these important differences, the
765 question raised by this study makes perfect sense: are the same processes all involved in all of
766 these methods?

767 Exposure to prism deviation, or Coriolis force-field allows the direct perception of
768 one’s own effector without any external force. As such, they entail extended sensory,
769 sensorimotor, and motor after-effects of the effector or of the axial components (eye, head).
770 This is the case not only in the particular context of the exposure, but in a broader spatial,
771 cross modal context and beyond the perturbation apparatus. These paradigms therefore imply
772 essentially context-independent processes. Force-field or rotated visuomotor feedback may
773 rather mostly imply context-dependent processes insofar as they generally only allow the
774 indirect perception of one’s own effector through a symbolic image of the effector (cursor, 3D
775 avatar) and imply the presence of an external force applied through a mechanical contact on
776 the reaching arm. As such they may also entail sensory, sensorimotor and motor after-effects
777 of the effector, but only within the narrow context in which they have been acquired. This
778 would support the fact that after-effects decrease sharply when the perturbation apparatus is
779 explicitly removed.

780 We reviewed that a possible two state model (fast vs slow process, explicit vs implicit
781 process) can explain compensations acquired to face prismatic deviation, as well as
782 visuomotor rotations or force-fields. In addition, the framework of internal representations
783 and sensory prediction errors also allows to explain compensations set up to counteract the
784 different perturbations. Thus, considering these similarities, the different paradigms indeed
785 would reflect similar sensorimotor processes on one hand. On the other hand, other form of
786 learning (model-free) are also involved in visuomotor rotations and force-field paradigms and
787 may rely more on a strategic behaviour compared with prisms or Coriolis force paradigms.
788 The presence of these model-free learning processes in “adaptation” paradigms questions
789 previous definitions of adaptation. In fact, the specific distinctions and potential overlaps
790 between these proposed involved processes are difficult to clearly define. For example, a
791 particular question is to understand the link between explicit processes proposed in the two
792 state model and other forms of learning: is the explicit component (i.e. strategic component in
793 prism studies) of adaptation a general learning mechanism, or are explicit and implicit
794 processes distinct components of adaptation that are independently from other forms of
795 learning? As suggested by Krakauer and Mazzoni (2011), learning and adaptation might rely
796 on a continuum on which several others subprocesses may overlap. A remaining question is
797 the degree of context-specificity associated with these subprocesses.

798

799 Another important question raised by this review concerns the notion of
800 generalization. The capacity to transfer compensatory adjustments beyond the exposure
801 context represents a crucial interest for clinically relevant purposes, as demonstrated by
802 the strong rehabilitation effect of prism adaptation in hemineglect patients (Jacquin-Courtois
803 et al., 2013; Rossetti et al., 1998). Over and above the aforementioned taxonomy issues and
804 lack of consensus across paradigms, the concept of generalization properties is characterized
805 by a large amount of heterogeneity both between and within each adaptation paradigm.
806 Although generalization depends considerably on specific exposure conditions, it appears that
807 body-centered perturbations (notably prisms) facilitate self-attribution of errors. As a
808 consequence, compensating for such perturbation leads to a possible broad generalization to
809 other context (i.e. others workspace), thus reflecting context-independent processes.
810 Conversely, attribution of errors to external causes (favoured by the existence of a handle-
811 induced contact cue and/or the presence of an interface in most force-field and visuomotor
812 rotation experiments) may lead to context-dependent compensations.

813 Nevertheless, this hypothetical relationship between error attribution and degree of
814 context specificity of elicited transformations arises from analysis of differences between
815 adaptation paradigms and needs future verification. In fact, a better understanding of the
816 notion of generalization needs to be developed in further work concomitantly with the concept
817 of credit assignment. A greater focus on the necessary conditions to elicit processes leading to
818 robust generalization could provide interesting findings in order to better distinguish the
819 relative contribution of processes. Specifically, elucidation of conditions required to trigger
820 context-independent processes is of great interest: developing a model specifically centred on
821 generalization properties could be very useful as a foundation for improved rehabilitation
822 therapies.

823 This review was limited to the analysis of the most prominent adaptation paradigms
824 studying reaching movements. Nevertheless, it is important to notice that other paradigms
825 have been used to study sensorimotor adaptation to in-depth prisms (Priot, Laboissière,
826 Plantier, Prablanc, & Roumes, 2011), to underwater viscous field (Macaluso et al., 2016) or to
827 modified gravity or weightlessness (Clément, Gurfinkel, Lestienne, Lipshits, & Popov, 1984;
828 Gaveau, Paizis, Berret, Pozzo, & Papaxanthis, 2011; Thomas Macaluso et al., 2017; Opsomer,
829 Théate, Lefèvre, & Thonnard, 2018; Pozzo, Berthoz, & Popov, 1995). Finally, error reduction
830 without perturbation (i.e. analysis of the time-series statistics of natural movement errors) has
831 also been investigated in order to highlight the properties of movement planning motor noise
832 vs movement execution motor noise (Beers, 2009).

833

834 To conclude, we posit that the comparative analysis of prism and other adaptation
835 paradigms reveals that different processes may actually be involved to counteract a
836 perturbation. Specifically, we suggest the possibility that paradigms involving an
837 interface/tool, a non-body-centred perturbation and a symbolic representation of the effector,
838 may favour compensations that are more context-dependent. Although this work provides a
839 holistic overview of comparison between different methods and highlights crucial
840 questioning, each level of analysis deserves to be more thoroughly investigated. Notably, even
841 though the neural substrates involved in “adaptation” paradigm are beyond the scope of this
842 paper, their investigation is necessary for an integrative approach. Future work should address
843 these limitations by providing more specific and exhaustive analysis, i.e. focusing on one
844 level of analysis (e.g. generalization).

845 Notwithstanding these limitations, this study offers a framework to better capture substantial
846 questions about sensorimotor plasticity processes and adaptation paradigms. The aim of the
847 present analysis was not to make a hierarchy of adaptation paradigms but rather to offer a
848 comparison between the different methods and to encourage future works to take into account
849 the specific characteristics of each one. Another important point was to emphasize the lack of
850 clarity and confusion that is still common around the processes of sensorimotor plasticity.
851 Though much progress has been made in understanding sensorimotor plasticity, more work is
852 still needed to achieve a unified picture of the process. Approaching the phenomena using
853 multiple methods of perturbation is crucial for making such progress. However, a central issue
854 is to be aware of the specific ways that constructs are defined for each paradigm.

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857

	Prisms	Coriolis	Force-field	Visuomotor Rotation
<i>Perturbation</i>				
<i>Altered modalities</i>	Visual	Visual and proprioceptive	Visual and proprioceptive	Visual
<i>Mechanical contact</i> ¹	No	No	Yes (manipulandum)	Yes (mouse)
<i>Visual interface</i>	No	No	Yes (screen)/No	Yes (screen)
<i>Body centered</i>	Yes	Yes	No	No
<i>Aftereffects</i>				
<i>Testing</i>	Post-exposure trials	Post-exposure trials	Catch trials Error clamp trials	Post-exposure trials “Blank” trials
<i>Distinct testing phase</i>	Yes	Yes	No (random test trials among exposure trials)	No (interspersed with exposure trials)
<i>Explicit removal of perturbation</i>	Yes	Yes	No (same apparatus)	No (same apparatus)
<i>Generalization</i>				
<i>With the same apparatus</i>	Yes (Harris, 1963)	Yes (Lackner & Dizio, 1994)	Yes (Kluzik et al., 2008)	Yes (Mazzoni & Krakauer, 2002)
<i>To natural movements</i>	Yes (Redding & Wallace, 2005)	Yes (Lefumat et al., 2015)	No (Cothros et al., 2006)	No available ²
<i>To the other arm/limb</i>	Yes (Choe & Welch,	Yes	Yes	Yes (Wang & Sainburg, 2004)

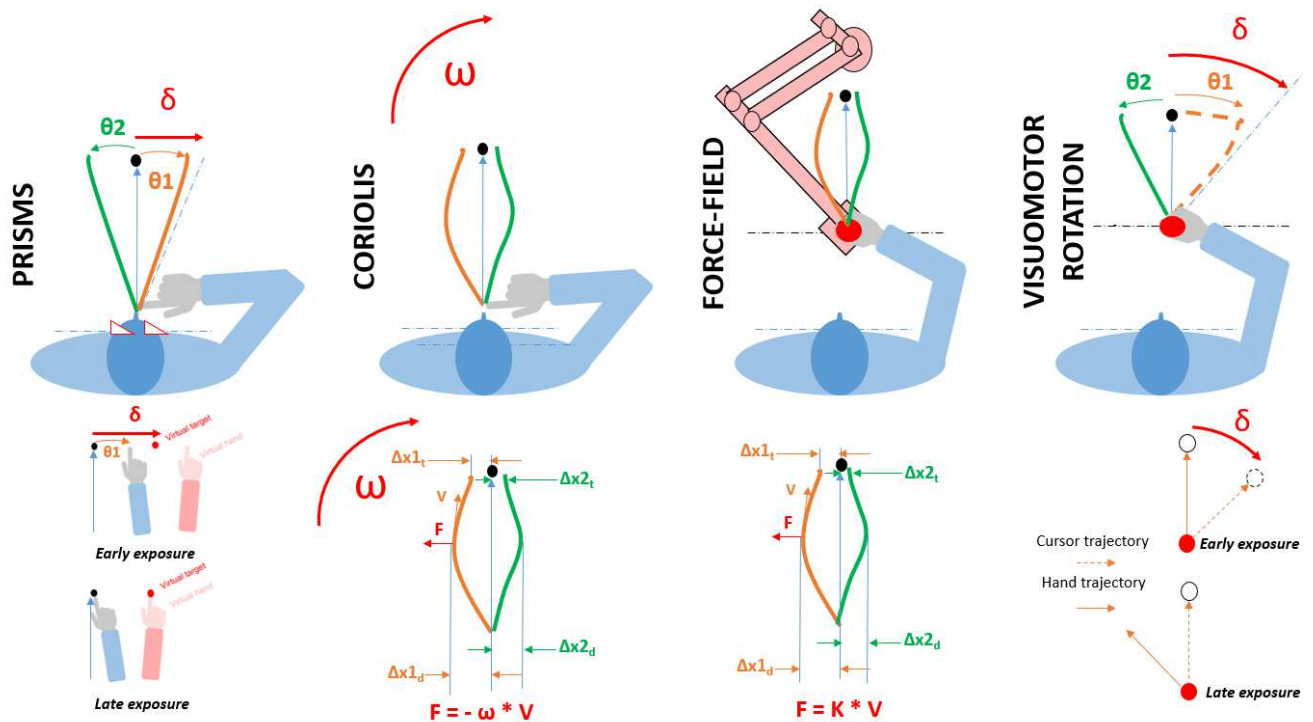
1974) /No (Prablanc et
al., 1975; Yin &
Kitazawa, 2001)

(Lefumat et al., 2015)

(Criscimagna-Hemminger,
2003)

/ No (Krakauer et al., 2000)

860 Summary of the main disparities among the different paradigms. Note. ¹ Refers to a contact between a device and the reaching arm. ² To our
861 knowledge, transfer of compensations induced by visuomotor experiments to natural movements has not been investigated.
862 *NB: references to the literature are provided to illustrate findings concerning generalization properties in a non-exhaustive manner.*



864

865 Figure 1. Illustration of the different types of perturbation and the observed movement errors.
 866 Movement errors during exposure are represented in orange and after-effects are represented
 867 in green. **1: Prisms:** prismatic lenses laterally deviate the visual field (i.e. both hand and
 868 target) by an optical shift (δ) while subject performs reaching movement (e.g. pointing).
 869 Virtual hand and virtual target (below) correspond to the images of hand and target seen
 870 through the prisms. θ_1 : initial error on first trials in the direction of the optical field. θ_2 :
 871 after-effects observed in the opposite direction (prisms removed). **2. Coriolis forces:** inertial
 872 forces (F) are applied on the moving arm while subject performs reaching movement in a
 873 rotation environment. ω is the angular rotation of the chair and V is the velocity of the moving
 874 hand. First reaching under perturbation is deviated to the direction opposite to the rotation.
 875 After-effects are a mirror image of initial deviation. Δx_{1_t} and Δx_{2_t} : terminal errors
 876 respectively during initial trials of rotation and post-rotation phase. Δx_{1_d} and Δx_{2_d} : dynamic
 877 errors respectively during initial trials of rotation and during post rotation phase. **3: Force-**
 878 **field:** a robotic manipulandum applies arm velocity-dependent orthogonal forces. Δx_{1_t} and
 879 Δx_{2_t} : terminal errors respectively during initial trials of force-field on and when the field is
 880 turned off (catch trials). Δx_{1_d} and Δx_{2_d} : dynamic error respectively during force-field on and
 881 when the field is turned off (catch trials). **4. Visuomotor rotations:** a computer interface
 882 alters the relationship between hand movement and on screen displayed cursor during
 883 reaching movement by imposing a clockwise rotation of 45° . θ_1 : feedback error observed on
 884 the screen during the first trials of exposure (rotated by δ°). θ_2 : after-effects : hand
 885 movement are deviated in the direction opposite to the rotation. Illustration of hand trajectory
 886 versus cursor trajectory (below). Note that subjects only see trajectories displayed on the
 887 screen, i.e. cursor trajectories.

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