

1 **The gravitational imprint on sensorimotor planning and control**

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15 **Abstract**

16 Humans excel at learning complex tasks and elite performers such as musicians or sportsmen develop
17 motor skills that defy biomechanical constraints. All actions require the movement of massive bodies. Of
18 particular interest in the process of sensorimotor learning and control is the impact of gravitational forces
19 on the body. Indeed, efficient control and accurate internal representations of the body configuration in
20 space depend on our ability to feel and anticipate the action of gravity. Here we review studies on
21 perception and sensorimotor control in both normal and altered gravity. Behavioral and modeling studies
22 together suggested that the nervous system develops efficient strategies to take advantage of
23 gravitational forces across a wide variety of tasks. However, when exposed to altered gravity, the rate of
24 strategy updating exhibited substantial variations from one experiment to another and sometimes led to
25 partial adjustment only. Overall, these results support the hypothesis that the brain uses a multimodal
26 and flexible representation of gravity effects on our body and movements. Future work is necessary to
27 better characterize the nature of this internal representation and the extent to which it can adapt to
28 novel contexts.

29

30 **Introduction**

31 Building a percept of the vertical axis, or equivalently defining which way is “up” or “down” is critical
32 to cope with gravitational forces and perform most physical actions. Multiple sensory cues can be
33 used to this purpose (Kheradmand and Otero-Millan 2019). For instance, one may assume that light
34 comes from above, which is used to interpret ambiguous images of shades (Adams 2007). But this is
35 a prior: light does not always come from above. Similarly, otolithic cues on their own cannot
36 dissociate between linear and gravitational acceleration. Therefore, this signal does not provide
37 unambiguous information about verticality. Considering this issue, it has been shown that humans
38 use an internal model to dissociate gravity from acceleration (Merfeld et al. 1999). However, gravity
39 does not only influence the vestibular system, and gravitational information is thus likely perceived
40 by integrating multiple sensory cues and their roles in many aspects of perception, movement
41 planning, and control.

42 For decades, many studies have suggested that the brain integrates the presence of gravity
43 to plan and perform efficient actions. Gravity is processed in a myriad of perceptual (Lathan et al.,
44 2000; Indovina et al., 2005; Zago and Lacquaniti, 2005a; Lacquaniti et al., 2015 for review) and motor
45 tasks (Chang et al. 2000; McIntyre et al. 2001; Papaxanthis et al. 1998a; White et al. 2016). Yet, the
46 body does not have a dedicated biological sensor to measure the direction of gravity. Instead, this
47 process, termed *graviception*, results from the integration of information from different modalities
48 such as visual, somatosensory, and vestibular signals (see Bock, 1998 for a review; Lackner and DiZio,
49 2000b; Lacquaniti et al., 2014). This information is used to adapt behaviour when task and/or
50 environment parameters change. Because changes of the mass or length of the moving limbs are
51 quite usual, for example through maturation or when holding different objects, adaptation to such
52 changes may be rather common. In contrast, it becomes much more challenging to understand how
53 the nervous system adapts to changes in gravity due to its influence on almost every sensory and
54 motor systems.

55 Although the hypothesis of a central representation of gravity has long been exploited in the
56 field, it is important to recall that earlier work on the impact of gravity was shown inconclusive,
57 owing to the large number of factors that differed across experiments (Bock 1998). It was argued in
58 this earlier review that studies of sensorimotor coordination in space should carefully consider a
59 number of confounding factors related to task-dependency, sample size, and context, which were
60 possible sources of discrepancies across collected results. The difficulty of gathering information due
61 to the diversity and extreme nature of testing environments remains. However, since the review of O.
62 Bock, converging evidence has emerged. Indeed, we now have at hand a larger number of studies

63 performed in broader range of testing conditions and performed in more constrained settings,
64 allowing us to better characterize the role of gravity in perceptual and motor systems.

65 In general, the studies reveal an efficient integration of gravity in perceptual decisions,
66 reaching and pointing, as well as a certain degree of flexibility in the motor system allowing
67 adaptation to changes in gravity. Interestingly, the speed at which participants adapt to changes in
68 gravity typically varies with the experimental context. However radical the change, a very short
69 exposure (a few tens of seconds) is sometimes sufficient to adjust motor commands, at least partially.
70 For instance, grip force is approximately scaled to the actual object dynamics in a matter of minutes
71 when exposed to hyper-gravity or weightlessness (Augurelle et al. 2003) or even swifter between
72 gravitoinertial environments (White et al. 2018). In other cases, however, the brain appears to use an
73 unadapted strategy over extended periods of time, in the sense that directional effects observed
74 under normal gravity persist while exposed to zero gravity (Mcintyre et al. 2001). Collectively the
75 studies reviewed here suggest the existence of a multimodal representation of gravity, which likely
76 supports rapid but partial adaptation in a broad range of motor tasks. In particular, we point to a
77 strong influence of somatosensory feedback, which possibly plays a role that is no less central than
78 the already recognized influence of vestibular signals for neural processing of gravity-related cues.
79 The manuscript is organized as follows: after presenting briefly the different experimental conditions
80 allowing one to study the influence of gravity on perception and action, we present results on the
81 perception of space and body orientation. Then we present results on sensorimotor control across
82 postural, reaching and object manipulation tasks performed under different gravitational contexts.

83

84 **Experimental Approaches**

85 Starting from the initial observations that the nervous system must account for inertial and
86 gravitational loads on the limb to perform straight paths with bell-shape velocity profiles (Atkeson
87 and Hollerbach 1985), several experimental approaches can be used to understand how the brain
88 deals with gravity. First, alterations of the context are controlled in such a way to simulate changes in
89 gravity for some but not all physiological parameters. These ground-based settings include
90 comparing a task executed along or perpendicular to gravity (Atkeson and Hollerbach 1985; Gentili et
91 al. 2007; Papaxanthis et al. 1998c) or underwater (Dalecki et al. 2012; Macaluso et al. 2016). While
92 these methods do not truly alter gravity per se, they constructively contribute to understand how the
93 nervous system deals with normal earth-gravity acceleration (1g). Another approach consists in
94 actually changing gravity in non-inertial environments creating hypergravity (>1g) or hypogravity
95 (<1g).

96 Hypergravity environments can be created on Earth by means of human centrifuges (DiZio
97 and Lackner 2002). Gravity can be increased by accelerating a gondola attached to a rotating gondola,
98 which induces a centripetal acceleration (a photo of a gondola is available in Figure 1 of White et al.,
99 2018). From the participants' standpoint, the vectorial sum between gravitational and centripetal
100 accelerations is equivalent to an increase in gravity. There are however two limitations to this
101 approach. The first is the presence of a gravitational gradient inside the gondola induced by the
102 proportional relationship between the rotation radius and the centripetal acceleration (see for
103 instance White et al., 2019). Because the radius is relatively short (typically two to nine meters), and
104 because the gondola is tilted to keep the local gravitational vector aligned with body axis, there is a
105 variation of the sensed gravity between the head and the feet. The second limitation is the presence
106 of Coriolis forces that affect movements orthogonal to the rotation axis and may also affect the
107 sensory apparatus. Such settings are therefore not ideal to focus on gravity per se, but clearly allow
108 studying adaptation to non-inertial environments in general and likely engage the same adaptation
109 mechanisms as a change in gravity. Several datasets reviewed below were collected in such
110 centrifuges.

111 Parabolic flights allow investigation of the effect of a variation in gravity by offering intervals
112 (20s) of ~1.8g before and after 0g phases (20s) for typical parabolic maneuvers (Shelhamer 2016).
113 This approach does not present the same limitations as Earth-based centrifuges because the
114 curvature of the aircraft trajectory is much smaller, therefore reducing the centripetal gradient and
115 Coriolis effects. Of course, a first limitation of parabolic flights in comparison with human centrifuges
116 is that achieving stable hypergravity levels is difficult, and gravity levels that can be safely produced
117 in a centrifuge (up to 4g) cannot be achieved so easily in the plane (generally 1.8g). Second, the
118 duration of each 0g phase is limited to about 20s (short-term exposure). Third, the alternation of 1g,
119 1.8g and 0g may also influence the adaptation measured across parabolas. Finally, there are often a
120 relatively low number of participants and trials per parabolic flight campaign. Typically, one
121 campaign comprises three flights with two to three participants per flight, yielding between six and
122 nine participants. Operational and budgetary constraints often make it difficult to perform the same
123 experiment during several campaigns, which sometimes hinders the ability to collect data with a
124 large number of participants.

125 Hypogravity environments for human experiments correspond to partial or free falling
126 (gravity < 1g), which cannot be generated on Earth for experimentations on humans. Two testing
127 environments have been used: parabolic flights and the orbiting International Space Station (ISS).
128 Parabolic flights offer sequences of 20s of weightlessness, or up to 32s for Mars (0.38g) and 25s for
129 Lunar (25s at 0.16g) environments (Pletser et al. 2012), which are repeated several times per flights
130 (e.g. 30 parabolas are usually performed during each flight). Parabolic flights allow performing

131 experiments with more participants than the number of astronauts in the ISS that can be involved in
132 a study. However, they only allow addressing short-term adaptation due to limited total time of
133 exposure and have similar constraints as those listed for hypergravity exposure. The ISS, in contrast,
134 offers a stable environment, but only hosts experiments with a very limited number of astronauts
135 who may not be representative of the general population as they undergo a highly demanding
136 cognitive and motor training program. Hence, understanding the role of gravity in motor control in
137 general requires considering data from distinct environments and contexts. The complexity of these
138 settings and their associated potential confounding factors sometimes challenge the interpretation
139 of the results. However, as we will see, there are consistent observations that emerge across tasks
140 and contexts that together provide insight into the neural basis of gravity-dependent aspects of
141 perceptual and motor tasks.

142

143 **Perception of our environment and our body**

144 This review essentially focuses on gravity-related sensorimotor planning and control. However,
145 because perception and action can hardly be dissociated, this section first briefly introduces the main
146 findings on perception. Gravity-related perception has been extensively reviewed elsewhere (for up
147 to date reviews see Lacquaniti et al., 2013; Jörges and López-Moliner, 2017; Dakin and Rosenberg,
148 2018; Lackner and DiZio, 2018). Changes in gravity are sensed through multiple sensory channels
149 prior to movement initiation (Bock, 1998; McIntyre et al., 1998; Lackner and DiZio, 2005 for review;
150 Tagliabue and McIntyre, 2011, 2014), and it is clear that movement success is contingent upon a
151 correct representation of the body configuration and of the movement goals in space. This contrasts
152 with standard force field experiments (e.g., velocity-dependent) performed in laboratories, where
153 the initial condition typically carries no information about movement dynamics since the
154 perturbation is applied during the movement (Lackner and Dizio 1994; Shadmehr et al. 2010 for
155 review; Shadmehr and Mussa-Ivaldi 1994). In altered gravity, adaptation starts prior to movement
156 because our senses convey information about the change in gravitational context. Perception of the
157 subjective vertical and estimate of self-orientation thus provide key information to build an internal
158 representation of the context before the action takes place.

159

160 *Perception of vertical axis*

161 Gravity strongly influences the subjective perception of verticality. Humans show an aesthetic
162 preference for subjective vertical (Gallagher and Ferrè 2018). Perception of vertical is also naturally
163 driven toward the body longitudinal axis (De Vrijer et al., 2008) in the absence of gravitational
164 information, which was conceptualized by the idiotropic vector model (Mittelstaedt 1983). In a

165 subjective orientation task performed during parabolic flights, Lackner and Dizio found that the
166 perceived vertical in the aircraft was maintained and even slightly improved under hypergravity,
167 whereas it was aligned with the body orientation under zero gravity (Lackner and Dizio 2009). This
168 result illustrated in Figure 1A is surprising because participants' body were physically rotated, and
169 thus the change in body orientation under 0g could be calculated by integrating acceleration signals
170 encoded in the vestibular system and re-align their pointing direction with the vertical of the aircraft.
171 The observation made by Lackner and Dizio that participants were unable to estimate the vertical
172 axis of the aircraft in 0g, in spite of acceleration levels much larger than perceptual thresholds,
173 suggested that instead of integrating rotational vestibular signals, they strongly relied on static
174 somatosensory feedback. Similarly, during microgravity episodes of parabolic flights or during a 9-
175 day spaceflight, participants reported their subjective vertical as mostly defined with respect to their
176 longitudinal body axis (Glasauer and Mittelstaedt 1992). Although subjected to large inter-individual
177 differences, these observations were further supported by data collected during Lunar and Martian
178 gravity contexts (de Winkel et al. 2012). In this study, irrespective of the static visual background
179 orientation, participants tended again to align the subjective vertical with the longitudinal body axis
180 for low values of gravity. This is in agreement with previous findings from Dyde and collaborators,
181 during parabolic flights, who reported a decreased influence of static visual tilt on the perception of
182 upright under microgravity conditions (Dyde et al. 2009). In a subsequent study, Alberts and
183 colleagues developed a Bayesian optimal integration model of this task that demonstrates
184 participants flexibly weigh visual panoramic and vestibular information based on their orientation-
185 dependent reliability (Alberts et al. 2016a).

186 Although results from short term exposure to microgravity argue for a body-centered
187 representation of the subjective vertical, it must be mentioned here that during long-term exposure
188 to microgravity, the impact of visual background on the perception of verticality has been shown to
189 be idiosyncratic (Kornilova et al., 1996; Lucertini et al., 2011; Krafczyk et al., 2003). Furthermore,
190 dynamic visual cues (animated video clip in which actors move) were shown more effective than
191 static ones (photos of the actor) to influence perception of the subjective vertical. Indeed, by
192 comparing the effects of static and dynamic visual cues, Jenkin and collaborators observed an
193 increased effectiveness of dynamic visual inputs in influencing the perceptual upright in microgravity,
194 in normal gravity and in hypergravity (Jenkin et al. 2011). In general, these studies point to a multi-
195 modal and context-dependent representation of verticality to which vestibular, visual and
196 somatosensory signals contribute through a weighted combination.

197

198 *Perception of body orientation*

199 Besides the subjective perception of the vertical, weightlessness also affects the perceived
200 orientation of the body in a way that seems attributable to a loss of somatosensory cues.
201 Interestingly, the perception of self “up” and “down” could be partially restored in microgravity
202 when applying localized pressure cues under the sole of the feet (Lackner and DiZio 1993, 2000a) or
203 by applying pressure to the chest (Clément et al. 2007).

204 Results collected on the ground corroborated these findings. It has been demonstrated that
205 the subjective body orientation in darkness is strongly affected when gravity-related somatosensory
206 cues are experimentally reduced by the use of a whole-body cast creating a more diffuse and
207 isotropic pattern of pressure around the body (Bringoux et al. 2003). Further, a study reported that
208 tilt-dependent noise determines the levels of both otolith and somatosensory signals to adjust the
209 weights of sensory inputs with tilt angle, revealing their partial dissociation (Alberts et al. 2016b). The
210 role of gravity-based somatosensory cues for body orientation can also be assessed through
211 perceptual responses given by a somatosensorily-deafferented patient (Bringoux et al. 2016). When
212 asked to detect self-tilt from vertical in different visuo-postural conditions (either facing real slow
213 body tilts and/or virtual tilts of the visual background), the patient never reported any tilt sensation
214 up to 18deg, contrary to control participants who detected self-tilt with a threshold of ~9deg on
215 average (Figure 1B). Thus, although the vestibular system is intact in this patient, the loss of
216 somatosensory feedback impaired tilt perception even in conditions when visual feedback about tilt
217 was provided. Other clinical studies provide evidence for adaptation mechanisms when the
218 vestibular system is impaired. For instance, in patients suffering from bilateral vestibular loss, the
219 proprioceptive system becomes dominant for visual processing (Cutfield et al. 2014). In the same
220 vein, another study adopted a Bayesian approach to show that bilateral vestibulopathy patients
221 reweight the non-impaired sensory information and rely more on visual and other non-vestibular
222 information than healthy controls to perceive spatial orientation (Medendorp et al. 2018). Other
223 previous research highlighted the perceptual impairment yielded by underwater immersion on
224 postural estimates and body orientation relative to the direction of gravity (Brown 1961; Massion et
225 al. 1995; Nelson 1968; Ross 1990). The diffuse and anisotropic application of pressure cues
226 underwater all around the body substantially alters gravity-related cues accessible to the
227 somatosensory system, hence degrading body orientation perception and control, despite intact
228 vestibular information. Overall, there is strong evidence for the idea that somatosensory signals are
229 key to the perception of body orientation, which has also been quantified by a Bayesian approach
230 (Clemens et al. 2011).

231

232 *Perception of object motion*

233 Gravity perception is not only used to define spatial orientation, but also to derive predictions about
234 the motion of moving objects during catching tasks (Jörges and López-Moliner 2017; McIntyre et al.
235 2001; Senot et al. 2005; Zago and Lacquaniti 2005b). The ball catching task provides clear insights.
236 Indeed, calculating the trajectory of the ball with and without gravity is straightforward which allows
237 for accurate predictions on the time of impact that can be compared to human preparatory activity.
238 If preparatory activity reflects anticipation of the time of impact, then, one can deduce that the time
239 course of the ball trajectory dependent on gravity was well anticipated. Based on these quantitative
240 predictions, it was concluded that humans use a prior about the acceleration of objects to
241 compensate for sensorimotor delays in the nervous system (Lacquaniti et al. 2013; Zago and
242 Lacquaniti 2008). Thus, the timing of action and the interaction with moving objects would be
243 impacted by an internal model of the laws of motion that necessarily depends on gravitational forces
244 (La Scaleia et al. 2015). Furthermore, information about head and body orientation contributes to
245 modelling the effects of gravity on a moving target (Ceccarelli et al., 2018; Claassen et al., 2016; La
246 Scaleia et al., 2019). Interestingly, the timing of catching actions for upward or downward catches
247 performed during short-term exposure to zero-gravity was reversed in a way that was consistent
248 with the activity of otolith receptors (Senot et al. 2012). In such tasks, the vestibular cortex was
249 selectively activated when object motion was consistent with gravitational acceleration. In contrast,
250 it was shown that visual areas in the brain were activated when the laws of motion were not
251 compatible with natural dynamics (Indovina et al. 2005; Miller et al. 2008).

252 These findings demonstrated a multimodal contribution to the perception of body
253 orientation and of the motion of moving objects in space. Multi-cue combination has long been
254 proposed to sub-serve both spatial orientation and object motion perception (Dokka et al. 2015;
255 Mergner et al. 1997; Senot 2005). In addition, recent findings highlighted that varying audio-tactile
256 cues about the dynamics of object's fall also impact perceptual estimates such as body height
257 (Tajadura-Jiménez et al. 2018). Importantly, gravity-related cues mediated by somatosensory inputs
258 appear to play a non-negligible role for self-orientation perception, which is expected to also impact
259 the planning and control of movements (see also Lackner and DiZio (2018) for a recent review on the
260 role of somatosensory inputs for postural control).

261

262 **Sensorimotor Control**

263 Beyond perception, gravity was found to also play a major role in the control of movements (Lackner
264 and DiZio 2000a; Pozzo et al. 1998). In light of these seminal studies, recent research has explored a

265 broad variety of tasks in different contexts, which together provided insight into the role of gravity in
266 sensorimotor control. Here we present a summary of the findings on goal-directed reaching and
267 object manipulation tasks, highlighting several properties of the neural mechanisms supporting
268 planning and control based on internal representation of the gravitational context.

269

270 *From Perception to Control*

271 As developed above, the fact that perception of our surroundings depends on gravity already
272 indicates that movement control must also take into account gravity. It is thus expected that the
273 nervous system must adapt motor commands to novel gravitational contexts. Initial studies showed
274 that the curvature of hand paths differed between upward and downward movements, which
275 suggested the presence of an internal representation of the impact of gravity on the formation of
276 end-point kinematics (Atkeson and Hollerbach 1985). Based on this observation, it was proposed that
277 the impact of altering gravity on the shape and curvature of pointing movements should provide
278 further insight into whether and how gravity was taken into account in the brain (McIntyre et al.
279 1998). Results from studies investigating multi-degree of freedom revealed an increased end-point
280 curvature for upward compared to downward reaching, reach to grasp, grasping, arm-hand drawing
281 and whole body sit-to-stand/stand-to-sit movements (Papaxanthis et al. 1998b, 2003, 2005;
282 Yamamoto and Koshiro 2014). In a similar vein relative time to peak velocity (which corresponds to
283 the ratio between acceleration time and deceleration time) was observed to differ for upward
284 compared to downward movement (Gentili et al. 2007; Papaxanthis et al. 1998c; Le Seac'h and
285 McIntyre 2007).

286 An internal representation of gravity within the central nervous system was supported by
287 evidence for transient changes in the velocity profile of pointing movements performed in
288 weightlessness, where directional differences (upwards vs downwards) decreased with practice
289 (Gaveau et al. 2016; McIntyre et al. 1998; Papaxanthis et al. 1998b, 2005). The striking observation
290 made across these previous studies was that directional differences in curvature and velocity profiles
291 persisted during the initial phase of exposure to 0g. If direction-dependent effects were simply linked
292 to mechanical interactions between gravity and anatomical constraints, then a change in gravity
293 should have had an instantaneous effect on hand trajectories. Indeed, recent studies highlighted
294 anatomical changes in the brain following exposure to microgravity (Lee et al. 2019; Riascos et al.
295 2019) or bed rest (Koppelmans et al. 2018). In contrast, the fact that they persisted in 0g, and
296 changed with practice, and the fact that up/down asymmetries occur very early in the movement
297 (Gaveau and Papaxanthis 2011), indicated that they reflected part of the planning of movement (as
298 opposed to a dynamic artifact during execution). This suggests that direction-dependent kinematics

299 emerge from anticipatory processes, or internal priors, based on an internal representation of gravity
300 (Gaveau and Papaxanthis 2011; McIntyre et al. 1998; Papaxanthis et al. 1998a, 1998b, 2005); which
301 likely represents an optimization of the motor plan to include the influence of gravity on the limb
302 (Gaveau et al. 2014, 2016; Wang and Dounskaia 2016).

303 To test whether graviception *per se* is the determining factor in defining “up” and “down” for
304 movement optimization, Le Seac’h and McIntyre (2007) had subjects perform point-to-point
305 movements when either standing upright or reclining in the horizontal plane (Le Seac’h and McIntyre
306 2007). They reported that head-to-toe and toe-to-head movements performed while reclining
307 resembled stereotypical horizontal movements when the eyes were open and vertical movements
308 when the eyes were closed. These observations suggest that motor planning can vary between an
309 allocentric frame of reference (aligned with gravity), when vision is allowed, to an egocentric frame
310 of reference (body-centered), when vision is prevented. Similarly, Sciutti and collaborators altered
311 the visual gravity and evoked changes in arm trajectory profiles, suggesting that the mechanical
312 effect of gravity on upper limbs could be anticipated from visual cues (Sciutti et al. 2012). Thus, there
313 is a visual contribution to the anticipatory processes that optimize movement planning with respect
314 to gravity.

315 Together, these results show that expectations about the direction and magnitude of gravity
316 are taken into account in the planning stage of a movement based on multiple sensory cues. Other
317 studies explored the role of sensory feedback more specifically by testing whether cues mediated by
318 somatosensory feedback could restore a sense of gravity and restore movement profiles comparable
319 with unperturbed contexts. Following this idea, Carriot and collaborators investigated the influence
320 of touch and pressure cues while participants pointed to their subjective horizon during microgravity
321 episodes of a parabolic flight (Carriot et al. 2004). Specifically, they applied pressure under the feet of
322 participants otherwise maintained steady in free floating by distributed bungee cords. The latter
323 condition yielded the final location of arm pointing movements toward the horizontal plane to be
324 closer to normal gravity observations, in comparison with those recorded in microgravity without
325 foot pressure.

326 With the intent of improving proprioceptive feedback, Bringoux et al. (2012) investigated
327 whether a gravity-related load applied to the limb helped reduce the constant error of reaching
328 movements performed during microgravity phases of parabolic flights with eyes closed. To that aim,
329 the authors applied a gravity-like torque to the shoulder joint of the moving arm by means of a set of
330 elastic bands attached to the limb. Specifically, the elastic set mimicked the net joint torque exerted
331 at the shoulder in 1g in the range of the different arm angular positions tested although it is clear
332 that the application of the torque to one point limits the analogy with gravity. As a result, movement

333 kinematics recovered stereotyped patterns as those exhibited on Earth, in spite of the fact that
334 participants (and their vestibular system) were immersed in zero gravity.

335 Conversely, if somatosensory feedback is used to infer gravity and influences planning as
336 demonstrated by providing artificial sense of gravity with joint torques or pressure to the body, then
337 it is conceivable that removing gravitational torque loads under normal gravity conditions could
338 evoke changes in movement trajectories without altering the gravitational context. Rousseau and
339 collaborators confirmed this prediction (Rousseau et al. 2016b). The authors asked participants to
340 achieve upward goal-directed arm movements in two natural conditions of initial steady-state arm
341 support (active vs passive). When the arm was “at rest” before movement execution, the relative
342 deceleration time substantially increased as compared to when the arm initial position was actively
343 maintained, and these effects could not be explained by changes in the peripheral motor apparatus
344 (i.e. background torque or muscle activation).

345 Collectively these results indicate that changes in gravity impacted movement trajectories,
346 but also interestingly that changes in somatosensory feedback simulating the presence or absence of
347 gravity evoked changes in trajectories that were consistent with a corresponding change in gravity.

348

349 *Adaptive Control of Reaching and Pointing*

350 While the evidence reviewed above highlighted neural processing of gravity-related sensory cues
351 during movement planning, the question arises as to whether these changes could be explained
352 under principles of optimal control. That is, do the re-organization of movement profiles reflect good
353 control solutions? In this line of research, several studies investigated how reaching movements of
354 the upper limb adapted to a transient or prolonged exposure to weightlessness by framing this
355 question in the context of optimal control. This allows expressing movement quality relative to
356 performances indices including physical variables such as gravity-related torques and was motivated
357 by the hypothesis of re-optimization of motor commands to account for novel limb or environmental
358 dynamics (Izawa et al. 2008).

359 More specifically, optimal control approach consists in calculating the best sequence of
360 motor commands with respect to a behavioral performance index and based on knowledge of
361 dynamics (Todorov 2004). The role of gravity in this framework has been considered either by having
362 a component of the performance that explicitly includes mechanical work in the cost function, or by
363 maintaining the same cost function such as a desired final position and velocity, while taking changes
364 in dynamics into account. The two approaches result in an optimal control law that accounts for
365 gravitational forces. In general, predictions obtained in these models have characterized velocity
366 profiles, patterns of muscle activity, and spontaneous movement paths while considering kinematic

367 costs, kinetic costs, and energy expenditures dependent on gravity (Berret et al., 2008, 2011, 2019
368 (for a review); Crevecoeur et al., 2009a; Gaveau et al., 2011, 2014, 2016). An important consideration
369 has been that movement properties changed in a way that was quantitatively captured by the model
370 simulations, which suggests that changes in behavior can be explained in theory. For example, an
371 inactivation principle was introduced to explain kinematic and muscle patterns of varied arm
372 movements performed in the vertical plane (Berret et al. 2008). Specifically, the *Minimum Absolute*
373 *Work* model proposes that simultaneous inactivation of both agonist and antagonist muscles
374 demonstrate the minimization of an energy-like criterion (Figure 2 A-B).

375 In this context, vertical reaching movements performed in normal or hypergravity were
376 simulated in an optimal control model penalizing end-point error and minimizing the integrated
377 control variable (Crevecoeur et al. 2009a), while accounting for the presence of a gravitational
378 torque pulling on the limb. The model predicted an increase in velocity profiles in response to the
379 change in gravitational torque during movement (Figure 2 C-D). This was not straightforward, as the
380 increase in shoulder torque could have slowed down movements. Interestingly, this pattern was
381 consistent with participants' behavior under hypergravity, suggesting that the change in behavior
382 from normal to hypergravity was indeed a good control solution.

383 A clear prediction from theoretical control models was that direction-dependent
384 asymmetries in the velocity profile of vertical movements should disappear (i.e. a longer relative
385 acceleration time for downward than for upward movements), similarly to the symmetrical
386 rightward and leftward horizontal movements performed on Earth; i.e. without gravitational torques
387 applied in the plane of motion (Gentili et al. 2007). This prediction was tested in two experiments
388 looking first at the velocity profile of movements when gradually varying orientation relative to
389 gravity (from horizontal to vertical), and second at vertical movements performed during parabolic
390 flights (Gaveau et al. 2016). Gaveau and collaborators observed a strong effect of movement
391 direction – i.e. the amount of gravity torque projecting in the plane of motion – on the arm
392 kinematics when movements were performed on Earth. Strikingly, Figure 2 E-H show that during
393 short-term exposure to weightlessness, there is a progressive disappearance of this direction-
394 dependent tuning towards direction-independent movements performed in the sagittal plane. These
395 results were quantitatively predicted by an optimal control model minimizing muscle effort (Figure 2
396 E-H); i.e. taking advantage of gravity effects to help accelerate or decelerate movements. Taking the
397 differences between upward and downward movement profiles as an index of adaptation, it was
398 observed that adaptation was nearly complete within about 5 parabolas (there were 12 trials per
399 parabola), as supported by theoretical values derived in the context of optimal control (Fig. 2F). This
400 study provided evidence for an optimization of the motor plan relative to the mechanical work of
401 gravity and for a re-optimization of this plan within minutes of exposure to weightlessness.

402 The study by Gaveau and collaborators (2016) highlighted that the difference between the
403 acceleration time and deceleration time of upward and downward movements vanished rapidly
404 during microgravity adaptation. However, this does not mean that movements were symmetric in
405 that respect; in absolute, the symmetry ratio (relative acceleration time with respect to movement
406 time) of a reaching movement may depend on other factors related to the experimental protocol.
407 For instance, Crevecoeur and collaborators (Crevecoeur et al. 2011) also found velocity profiles
408 under microgravity that were similar across up and down movements but whose symmetry ratios
409 (mean \approx 0.45) were slightly smaller than those observed by Gaveau and collaborators in microgravity
410 after adaptation (mean \approx 0.48) or by Gentili and collaborators for horizontal movements (mean in
411 [0.48, 0.5]). Other studies have also reported highly skewed velocity profiles for horizontal
412 movements under normal gravity and during parabolic flights (Crevecoeur et al. 2014), as well as
413 during prolonged exposure to weightlessness in the former orbiting MIR station (Mechtcheriakov et
414 al. 2002). These observations of varying symmetry ratios for horizontal movements may relate to
415 instructions about movement accuracy, as they increased with visual feedback, and thus with more
416 stringent control of movement end-point (Langolf et al. 1976; Mechtcheriakov et al. 2002; Soechting
417 1984). These impact of changes in gravity on horizontal movements also indicated that the internal
418 representation of gravity is not simply used to separate gravity related torque from dynamic ones in
419 the formation of motor commands (Atkeson and Hollerbach 1985; Flanders and Herrmann 1992;
420 Hollerbach and Flash 1982), because changes in gravity also influence horizontal movements where
421 dissociation should leave hand trajectories unaffected.

422 Another finding across several studies is a general tendency for movement slowing for both
423 vertical and horizontal movements performed in weightlessness (Crevecoeur et al. 2011, 2014;
424 Mechtcheriakov et al. 2002; White et al. 2008a). The reason why movement slowing occurs is still
425 unclear, although it likely relates to maintaining movement accuracy instead of a sensorimotor
426 deficit (Mechtcheriakov et al. 2002). Theoretical predictions have shown that slowing could mitigate
427 the impact of uncertainty in the internal models of limb dynamics (Crevecoeur et al. 2010a) or
428 optimize the altered dynamics of the task by exploiting system properties such as the resonant
429 frequency when the movement is rhythmic (White et al. 2008a). It was also shown that a mismatch
430 between expected and actual gravity in the internal model of limb dynamics, linked to an error in the
431 estimation of the mass of the limb or of the objects that we manipulate, could at least partially
432 account for movement slowness in microgravity (Crevecoeur et al. 2014). In the latter study, it was
433 hypothesized that a change in weight could be incorrectly attributed to a change in mass, which is a
434 reasonable prior given a life-long experience on Earth. When gravity is not constant however, this
435 incorrect attribution of an increased weight to the mass generates a mismatch between the true and
436 expected masses, therefore impacting the calibration of motor commands and eventually generating

437 motor errors. In fact, the latter study also provided strong evidence for an integration of gravity in
438 movement planning, as the kinematics of horizontal movements was strongly perturbed by the
439 alternating gravitational phases, revealing a cross-talk between gravity and movement planning even
440 in a direction where the dynamics was unchanged (Fig. 2 I-K). Finally, by adopting a different
441 approach, a recent study showed that adiabatic invariants, which determine a property of a system
442 that stays approximately constant when external changes occur slowly - such as gravity - also explain
443 these findings (Boulanger et al. 2019).

444 The hypothesis of re-optimization was also exploited to understand reaching control towards
445 targets located beyond arm length during parabolic flights. In normal gravity, forward bending of the
446 trunk is limited by balance control. As a result, participants tend to use coordinated lower limb and
447 trunk flexion to avoid destabilizing the body (Berret et al. 2009). Under zero gravity, this constraint
448 disappears, relaxing constraints on some degrees of freedom, hence allowing participants to lean
449 forward (Casellato et al. 2012; Macaluso et al. 2017). These results were interpreted as an
450 optimization of postural control in the absence of gravitational constraints. Interestingly, recent
451 results collected in simulated weightlessness (underwater) reproduced the same behavior (Macaluso
452 et al. 2016), but warranted a more nuanced interpretation (Figure 3). Indeed, forward motion of the
453 center of mass were observed when neutral buoyancy was applied to each joint individually, but not
454 when neutral buoyancy was applied to the center of mass (Macaluso et al. 2016). Thus, relaxing
455 balance control of the center of mass is not sufficient to evoke the behavior observed during
456 parabolic flights by Casellato and collaborators. The tendency to lean forward when reaching beyond
457 arm's length could be more deeply rooted in the details of the mechanical interactions with the
458 environment at individual joints. Notice also that participants (and their vestibular system)
459 performing the task under water were submitted to normal gravity condition, which points again to a
460 possible role of proprioceptive feedback in the processing of gravity-related sensory cues since visual
461 information was available in all contexts.

462 In all, changes in gravity have multifaceted effects on sensorimotor control of reaching and
463 pointing. On the one hand, there is evidence for an efficient use of gravity to accelerate or slow
464 down the movement; i.e. for an optimization of motor commands while considering the gravitational
465 torques acting on the limbs (for instance, induced to some degree by elastic bands). On the other
466 hand, changes in gravity also impact movements where it should not, as for horizontal movements
467 performed under zero gravity, which also suggests a perturbation of gravity-dependent motor
468 commands. Teasing apart these two hypotheses and quantifying their contribution (re-optimization
469 versus perturbation) is a difficult but exciting question for future work. In any case, all observations
470 collectively point to an internal representation of gravity-related torques on the body, and suggest
471 that the underlying model-based control changes quickly, be it in a naive or efficient way.

472

473 *Control of Precision Grip during Upper Limb Movements*

474 Motor behavior during object manipulation tasks was also investigated to challenge the use of an
475 internal model of gravity, based on the premise that the control of grasping forces applied to a held
476 object reflects anticipation, and thus internal knowledge, of self-generated motor commands
477 (Flanagan and Wing 1997). In normal gravitational conditions, we can seamlessly stabilize an object
478 in a precision grip configuration (thumb opposing index finger). To achieve this action, the grip force
479 must be adjusted such that the induced static friction force (through Coulomb's law) exceeds the
480 destabilizing load force (Cole and Johansson 1993). The load force can be broken down into two
481 components: the gravitational force (or equivalently the object weight, which, for an object of mass
482 m equals $m\vec{g}$), and an inertial force ($m\vec{a}$) that results from accelerating the object with acceleration
483 \vec{a} . During manipulation tasks, the central nervous system needs to counter the load profile that
484 results from the acceleration of the arm and the background gravitational term.

485 Under normal gravity conditions, the load force is well anticipated in normal manipulation
486 tasks and when it is arbitrary formed, highlighting internal prediction about the self-generated
487 constraints (Flanagan and Wing 1995, 1997). This control becomes challenging when movements are
488 performed under altered gravity, where the weight changes while the inertial load for a given
489 acceleration remains constant.

490 A first study by Hermsdörfer and collaborators investigated grip force adjustments during
491 stationary holding of an object (i.e. without arm movements), and found that the static level of grip
492 force followed both the increase and decrease in object weight induced by parabolic flights
493 (Hermsdörfer et al. 1999). These authors also reported that grip force gradually decreased across a
494 few parabolas leading to a reduction of the safety margin. This indicated that the adjustments
495 involved some habituation to the novel environment. Other investigations that tested human's
496 ability to generate specific force profiles in altered gravity highlighted some limitations in the control
497 of the force. For instance, in microgravity, even after several trials, participants overestimated a
498 target force displayed on a screen that they were instructed to reproduce (Mierau et al. 2008). In
499 another study, participants produced isometric force pulses of prescribed intensities in 3g (Göbel et
500 al. 2006). During exposure, the force profile was much larger than in normal gravitational conditions,
501 especially during the first 100ms. The later part of the force profile demonstrated that some adaptive
502 reprogramming occurred using feedback-based corrections.

503 In the context of vertical oscillatory movements, the load force oscillates around the object
504 weight, which, under microgravity, generates load force peaks of alternating sign since the weight is
505 zero. At the top of the trajectory, the object tends to keep moving upwards. This situation is only

506 experienced in normal gravity for high and unnatural levels of downwards acceleration. Previous
507 work reported that, in such task, the grip modulation doubled frequency in comparison with normal
508 gravity, likely to counter the inertial peaks occurring both at the top and bottom of cycles (Augurelle
509 et al. 2003; Nowak et al. 2000). These studies also reported synchronized modulation between grip
510 force and load force, with even a small lead for the grip force, compatible with anticipation
511 (Augurelle et al. 2003).

512 Adaptation or habituation was also observed when comparing the performance of naïve
513 participants with that of experienced ones (>100 parabolas each). Naïve participants clearly exhibited
514 a gradual refinement of the grip-load coupling gain (Figure 4, top row), which quickly stabilized
515 within 5 to 10 parabolas (3min), and eventually compared to the performance of experts. In contrast,
516 perfect synchronization of both forces was observed in the two groups from the outset. An
517 important observation made in these studies was that the minimum grip-to-load ratio at the end of
518 the experiment, indicative of the safety margin, tended to be constant across gravitational phases
519 (Augurelle et al. 2003; Nowak et al. 2000). In subsequent studies where the load was varied across
520 conditions by altering the movement frequency, the object mass or the gravitational context, White
521 and collaborators showed that the grip force was well adjusted to the actual load (White 2015; White
522 et al. 2005). Although distinct arm commands generated similar load forces, the grip force remained
523 adjusted to the load force, and the force ratio was preserved across conditions (White et al. 2005).
524 Furthermore, the arm motor command and the grip motor command can be adjusted separately
525 (Bringoux et al. 2012b). Collectively these observations lead to the hypothesis that the motor system
526 adjusts the grip commands based on an internal model of the limb and object dynamics, which
527 includes knowledge of the gravity field. This kind of predictive mechanisms has been suggested as a
528 general theory of sensorimotor control (Kawato 1999) Shadmehr, 2008}. The important addition of
529 studies on changes in gravity was to incorporate the action of gravity in the internal models.

530 Point-to-point movements performed with a hand-held load during parabolic flights revealed
531 a more nuanced story in comparison with oscillatory movements, possibly due to the distinct neural
532 substrates supporting discrete and rhythmic motor tasks (Schaal et al. 2004). In these tasks,
533 inexperienced participants performed movements in weightlessness towards visual targets, and
534 separated by short intervals of stationary holding (static phases). The grip force measured during the
535 static phases displayed a slow decrease across parabolas, and only stabilized beyond the 10th
536 parabola (Crevecoeur et al. 2009b, 2010b; Giard et al. 2015). In contrast, these studies reported a
537 rather fast adjustment of the grip scaling with changes in load force, that paralleled the presence of
538 both positive and negative load force peaks across individual movements, which scaled in amplitude
539 with the inertial loads (Crevecoeur et al. 2010b; Nowak et al. 2001). Indeed, the dynamic modulation
540 of grip force during movement tended to stabilize quicker (<7 parabolas, (Crevecoeur et al. 2010b)),

541 or even exhibited no evolution across parabolas (Crevecoeur et al. 2009b), which may thus be
542 partially decoupled from the stabilization of the overall grip level, including the static component,
543 which typically takes more than 10 parabolas (> 3 mins).

544 The grip-load coupling during point-to-point movements also revealed instantaneous scaling
545 of motor gains with changes in gravity. Under hypergravity, the weight increases but the inertial
546 loads for a given acceleration do not. Thus, it would be reasonable to expect an increase in baseline
547 level of grip force without changes in modulation gain, as the inertial loads remain the same.
548 Surprisingly, this was not the strategy adopted by participants: in fact, the grip modulation gains also
549 increased in hypergravity, in addition to the level of grip force developed during stationary holding
550 (Crevecoeur et al. 2010b). These observations suggest that in this task, a rather automatic coupling
551 exists between the force developed during stationary holding and the force modulation associated
552 with movement. Horizontal point-to-point movements (relative to the vertical gravity) further
553 illustrated this effect. Although there is no change in environmental dynamics along this axis, motor
554 gains for both limb and grip force control paralleled the change in vertical gravity (Crevecoeur et al.
555 2014). These observations clearly contrast with the fact that the grip-load modulation gain tends to
556 decrease when the baseline level of grip force increases (Flanagan and Wing 1995). Thus, the
557 increase in baseline force was associated with a concomitant increase in modulation gain, both of
558 which depended on gravity.

559 Recent human centrifuge datasets provide complementary observations about the coupling
560 between grip and load forces. It was shown that humans were able to adapt motor commands in a
561 lifting task between 1g, 1.5g, 2g, 2.5g and 3g within a few trials (White et al. 2018) and in an
562 oscillatory task in the 1.25g-2.4g interval (Barbiero et al. 2017). The authors reported that grip force
563 was overall adjusted from the first trial in the new, never experienced, context. However, small
564 changes across trials also demonstrated that further adjustments occurred. Indeed, grip force in the
565 very first trial was sometimes larger than in subsequent trials. A simple model that attempted to
566 predict the value of grip force in the next environment from expectations was accurate when gravity
567 in the new environment increased and failed when gravity in the new context decreased (White et al.
568 2018). This study suggests that in unfamiliar dynamic environments, grip force regulation could be
569 characterized by a successful anticipation of the experienced environmental condition interacting
570 with more cognitive mechanisms, possibly linked to risk aversion. This contrasts with expected
571 leaning curves indicative of motor adaptation observed in human reaching experiments (Wolpert et
572 al. 2011).

573 A recent study also showed that practicing a manipulation task under Mars-, and Moon-
574 gravity benefited to the scaling for grip force performed under micro-gravity (Opsomer et al. 2018)
575 (Figure 4, bottom). Indeed, the grip-load relationship under zero gravity appeared less disrupted

576 when manipulation was preceded by phases of hypogravity in comparison with the coordination
577 pattern and safety margins reported when naïve participants manipulate objects under zero gravity
578 for the first time (Augurelle et al. 2003). In other words, the experience of a previous hypogravity
579 context helped to adjust grip force in a new hypogravity environment, by reducing the safety margin.
580 Yet the overall safety margin remained higher than under normal gravity, which is indicative of
581 incomplete habituation. This suggests that these rapid behavioral changes are led by direct, or
582 automatic scaling mechanisms calibrated by the effect of gravity on the body, which interact with
583 other factor linked to volitional control. These observations emphasize again the importance of the
584 information available before the action takes place.

585 Evidence for rapid but uncompleted adaptation was reported in a collision task, where naïve
586 participants were instructed to hit a small target covered with foam to evoke impact loads (White et
587 al. 2011, 2012). The authors reported that, during zero-gravity phases of parabolic flights, the grip-
588 load coupling was well adapted to the inertial load as for point-to-point movements (transport
589 phase). However there remained a tendency to squeeze the object harder when colliding against the
590 upward target, despite there was no increase in the risk of dropping the object in this direction as
591 under normal gravity. Consistent with this interpretation, this strategy was employed in normal and
592 hypergravity. Thus, the coordination pattern during movement indicated adaptation as in the
593 previous point-to-point experiments, but differences in strategies across upward and downward
594 collisions also reflected directional and likely gravity-dependent biases in motor planning.

595 To summarize, grip-load coupling under altered gravity revealed task-dependent changes
596 with again multiple sides to the same story. In general, there was an efficient adjustment of the grip
597 control pattern within the first parabolas, with the novel load profiles that resulted from changes in
598 gravity induced by parabolic flights or by centrifugation. Yet, point-to-point movements and
599 collisions indicated also indicated the presence of rapid and perhaps automatic scaling of motor gains
600 (e.g. influence on horizontal point-to-point movements), along with the persistence of directional
601 biases observed under normal gravity such as movement asymmetries, and higher safety margins.

602

603 **Neural processing of gravity**

604 Primary sensory areas have evolved to process information from physical variables encoded in
605 dedicated sensory organs. For instance, information about light encoded in retinal cells converge to
606 primary visual cortex. Likewise, primary somatosensory cortex is the major hub to collect
607 somatosensory feedback. In contrast, there is no dedicated sensory organ for gravity, making
608 perception of the gravity field multisensory in essence. It is therefore expected that the

609 representation of the gravity field emerges through a distributed processing in associative regions or
610 networks.

611 It is clear that the question of how neural activity encodes or uses gravity faces insuperable
612 technical difficulties. For instance, it is to date impossible to acquire imaging data during a parabolic
613 flight. Studies performed on ground mainly manipulate movement directions to infer the impact of
614 gravity on motor control. They intrinsically bring a confounding factor: changes relative to gravity are
615 linked to changes in movement directions. Portable techniques such as EEG or fNIRS can be brought
616 in flight but these measurements may be impacted by the harsh environmental instability inherent
617 with parabolic maneuvers. As a result, current knowledge on gravity-related neural processing may
618 appear sparse or based on approaches that are too context-dependent to draw meaningful and
619 clear-cut conclusions. Nevertheless, there is evidence for neural activity specific to gravity as
620 suggested below.

621 Populations of neurons located in several brain areas have been proposed to perform the
622 computations necessary to encode physical variables of the external world, such as linear
623 acceleration (Angelaki et al. 1999; Angelaki and Dickman 2000; Laurens et al. 2013a). Notably, firing
624 rates of cells in the anterior thalamus, the vestibular nuclei and in the cerebellar fastigial nucleus are
625 tuned to head movement relative to gravity (Angelaki et al. 2004; Laurens et al. 2013b, 2013a, 2016).
626 Furthermore, functional MRI studies (in ground settings) found activation of a “vestibular network”
627 including the insular cortex (Lacquaniti et al. 2013) and the temporo-parietal junction (Kheradmand
628 and Winnick 2017) during visual processing of vertical motion under gravitational attraction
629 (Indovina et al., 2005; Miller et al., 2008 and Lopez et al., 2012 for a review). These experiments
630 suggested that the brain processes the trajectory of a free-falling object in such a way to anticipate
631 its acceleration. The insula at the core of this network seems to be a critical node to integrate
632 gravity-relevant signals. Indeed, the insula is activated in various tasks that strongly rely on gravity
633 such as active balance (Karim et al. 2014) but also during mental imagery of balance (Jahn et al. 2004;
634 Malouin et al. 2003). Dieterich and her team made several other contributions to this quest. In one
635 recent study, they found that the perception of verticality is impaired by electrical stimulation of the
636 parietal lobe (Kremmyda et al. 2019). A few years ago, the authors showed that otolith-dominated
637 graviceptive vertical perception is modulated by deep brain stimulation of the nucleus ventralis
638 intermedius which indicates its involvement in vertical perception (Baier et al. 2017). The topology of
639 the vestibular network definitely relies on several critical nodes.

640 While several investigations addressed the question of the internal representation of gravity
641 through visual information (Indovina et al. 2005; Lacquaniti and Maioli 1989; Maffei et al. 2016;
642 McIntyre et al. 2001; Zago et al. 2004; Zago and Lacquaniti 2005c), its neural bases in the absence of
643 vision remains elusive. However, in light of the behavioral evidence reviewed above, it is reasonable

644 to expect the existence of a representation of gravity dependent on somatosensory feedback, likely
645 through an internal model of external forces acting on the limb. Consistent with this idea, White and
646 collaborators found in fMRI studies a selective insular activity during a wrist flexion task when
647 aligned with the vertical, with no visual guidance. Insular activity only emerged in vertical but not
648 horizontal wrist movements (Rousseau et al. 2016a). Furthermore, whether the action was real or
649 mentally simulated also influenced the sub-area of the insula that was active. Actual movements
650 highlighted the posterior insula. In contrast, mentally simulating the movement engaged a more
651 anterior part of the insula (Rousseau et al. 2019). Another recent elegant study, however, suggests
652 that motor imagery of object motion does not rely on an internal model of gravity, but instead
653 resorts to a simulation of visual motion, probably involving mostly visual areas (Gravano et al. 2017).
654 Therefore, it is possible that different parts of the insula may process gravity-relevant feedback in
655 simulated or produced actions that involve the body while external simulation of the environment
656 may exploit other pathways.

657 Several studies have also measured brain activity *during* weightlessness using EEG (Cebolla et
658 al. 2016; Cheron et al. 2006, 2014). Alpha rhythms (8–14 Hz) reflect inhibition of sensory information
659 (Foxe and Snyder 2011). Cebolla and collaborators (Cebolla et al. 2016) asked astronauts to execute a
660 low-level visuo-attentional task consisting in controlling the position of a spacecraft in virtual reality.
661 The EEG analysis revealed that the cerebellum and other areas of the vestibular system took over the
662 increased demand for postural stabilization and error corrections while free-floating. One recent
663 study also used resting state fMRI and reported alterations in vestibular and motor-related regions in
664 a single astronaut’s brain after 6 months spent in weightlessness (Demertzi et al. 2016). A decreased
665 in functional connectivity of the insula was found, consistent with the idea that the insular cortex is a
666 pivotal region for processing gravity-related cues, and that exposure to weightlessness reduced the
667 weight of its links with other regions.

668 Mirroring the complex effects of changes in gravity on behavior, experimental evidence
669 about the neural processing of gravity-related signals for perception and control points to a broad
670 and distributed network including cerebellum, sensorimotor, vestibular, and insular cortices. Indeed,
671 in a rod orientation task, recent results have revealed the superiority of dynamic visual cues over
672 static ones in eliciting visual disturbance of verticality in cerebellar patients (Dakin et al. 2018). These
673 results echo similar observations on the ineffectiveness of static visual cues versus the effectiveness
674 of dynamic visual cues in evoking postural responses in cerebellar patients (Bunn et al. 2015;
675 Tarnutzer et al. 2008). Other recent results further confirm that cerebellar function is critical for
676 perception of spatial orientation (MacNeilage and Glasauer 2018). The next steps to deepen our
677 understanding of the neural bases of adaptation to changes in gravity will require to address

678 important methodological issues such as techniques to measure (deep) brain activities directly in the
679 new gravitational environment.
680

681 **Conclusions and Perspectives**

682 To synthesize, the evidence reviewed above suggests the presence of a multimodal internal
683 representation of gravity used to probe our environments, to interact with objects, to plan, and to
684 control movements. studies performed in altered environments have unanimously highlighted rapid
685 albeit sometimes partial habituation to changes in gravity, for instance based on unnecessary scaling
686 of motor gains. On the one hand, several pieces of evidence have provided a descriptive account of
687 the impact of gravity on perception and motor control, such as changes in movement kinematics or
688 altered grip-load relationships. In some cases, changes are meaningfully linked to a change in gravity,
689 such as an increase or decrease in grasping forces under hyper or microgravity respectively. However,
690 other observations such as movement slowing, changes in coordination patterns, or statistical
691 parameters describing grip-load relationships, remain puzzling. On the other hand, several groups
692 have attempted to provide principled accounts of gravity-related changes in behavior, such as in ball
693 catching and in reaching or pointing control, where an impact of gravity can be calculated. Taking
694 descriptive and theoretical results together suggest that the internal representation of gravity is
695 multimodal and flexible.

696 The precise nature and properties of this internal representation is not fully understood yet.
697 First, experiments performed under altered gravitational conditions highlighted rapid adaptation, but
698 also biases indicative of partial habituation observed during the whole (often short-term) exposure
699 to weightlessness. Second, the absence of dedicated sensory organs and neural area points to a
700 distributed processing of gravity cues for perception and control. In particular, we emphasize the role
701 of somatosensory feedback, which, in light of its influence on planning and control, may serve as a
702 calibration signal conditioning our perception and the scaling of motor commands, in addition to
703 visual, vestibular and internal (prior) information.

704 How can the rapid but partial adaptation be interpreted? From a conceptual perspective,
705 these results can be captured by considering a parametric representation of gravity in the brain,
706 which impacts perception and control. With such a parametric representation depicted in Figure 5,
707 the partial adaptation can result from inference about gravity, which, in a probabilistic setting, can
708 vary to some extent due to sensory cues, but not entirely due to strong priors about the invariant
709 nature of gravity on Earth. Here we mean a Bayesian prior about gravity, referring to a value used as
710 default, independent of sensory cues. Following changes in gravity, a posterior estimate of this
711 parameter is formed based on a combination of the prior and the sensory signals. If the prior is
712 narrow about the value of Earth gravity (i.e. our estimate about 1g is accurate), consequence of a
713 life-long experience, the posterior estimate will exhibit a bias towards 1g. As a result, a partial motor
714 adaptation is expected. It should be noted that this conceptual model potentially involves daunting

715 calculations. The reason is that each sensory modality may provide information about gravity in their
716 own encoding scheme and affected by different delays. It was recently suggested that multisensory
717 integration during movement considers different delays (Crevecoeur et al. 2016), but this aspect is
718 still debated (Cluff et al. 2015; Oostwoud Wijdenes and Medendorp 2017), and the processing of a
719 massive change as induced by altered gravity can be a very challenging task.

720 Another potential source of sensorimotor biases could be the presence of rather automatic
721 circuits such as a direct mapping between loads and motor commands. In this framework, the partial
722 adaptation could be explained by the expression of both inflexible and adaptive mechanisms, much
723 like reflex responses to perturbation involve both automatic and flexible components (Crevecoeur
724 and Kurtzer 2018; Scott 2016; White et al. 2008b).

725 We believe that future work, for instance following long-term exposure or based on virtual
726 reality, will shed light onto this important question. Indeed, in the case of probabilistic inference, it is
727 conceivable that priors about 1g will change over longer exposure (~months). Likewise, the use of
728 virtual reality to perturb participants' prior may reveal how much (biased) inference versus inflexible
729 neural circuits account for partial adaptation to altered gravity. There also remain questions about
730 the nature of the internal representation of gravity: although it is clearly based on multi-modal
731 sensory cues, it is unknown whether its behavioral expressions result from multi-modal interactions,
732 or whether a unified percept of gravity is constructed in the brain. Characterizing how distributed
733 neural processing gives rise to gravity-dependent behavior is an exciting challenge for prospective
734 studies.

735

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743

744 **Figures**

745

746 **Figure 1**

747 Perception of external and body orientation. **(A)** Subjective vertical as a function of head orientation
748 for supine subjects in three different gravitational backgrounds. From Lackner & DiZio (2009).
749 Participants were lying in a rotating bed and were instructed to report the direction of vertical of the
750 aircraft after rotation of the bed **(B)** Mean self-tilt detection thresholds from a vertical orientation as
751 a function of experimental conditions for Controls and a deafferented patient (GL) deprived of
752 somatosensory feedback. Conditions are: Backward rotation of the visual scene (Sbwd), forward
753 rotation of the body without visual scene (Bfwd), forward rotation of the body and visual scene
754 (BfwdS), and forward body rotation without rotation of the scene (BfwdSbwd). Thresholds for the
755 deafferented patient were arbitrary set at the minimal value over the manipulated range of tilt (thin
756 line at 18 deg) as she never felt any tilt sensation up to the largest tilt angle across the different trials
757 in all the conditions she was exposed to. From Bringoux et al. (2016).

758

759 **Figure 2**

760 Adaptation of reaching movements across various gravity levels. **A-B** (adapted from Berret et al.,
761 2008). Theoretical velocity profiles and control signals derived in the context of optimal control by
762 taking positivity constraints of agonist-antagonist pairs of muscles. The model predicts an interval
763 during which control is equal to zero (highlighted). **(B)** Velocity and EMG profiles of Deltoid Anterior
764 (DA), Deltoid Posterior (DP), Biceps (BI) and Triceps (TR) muscles during vertical movements. The
765 interval of inactivation expected in the model is also highlighted. **C-D** (adapted from Crevecoeur et al.,
766 2009) Optimal velocity profiles for vertical movements under normal and hyper-gravity condition.
767 The model was the rotation of a rigid segment with linear actuator. Observe the predicted increase in
768 velocity. **(D)** Measured velocity profiles under normal and hyper gravity from one representative
769 participant. **E-H** (adapted from Gaveau et al. 2016) Participants' initial position and positioning of the
770 3 targets in the sagittal plane. Eleven participants performed fast and visually guided mono-articular
771 upward and downward arm movements (shoulder rotations in the sagittal plane) under normal
772 gravity (1g) and microgravity conditions (0g) during a parabolic flight (parabola 1, P1 to parabola 5,
773 P5). **(F)** Symmetry ratios (acceleration time / movement time) predicted by the Minimum Smooth-
774 Effort model in 1g and in 0g conditions. **(G)** Symmetry ratios experimentally recorded before (1g) and
775 during adaptation to 0g (P1 to P5). **(H)** Mean velocity profiles, normalized in amplitude and duration.
776 Qualitative comparisons between upward and downward arm movements illustrate the progressive
777 decrease of directional asymmetries when subjects adapted to the new microgravity environment. **I-**

778 **K** (adapted from Crevecoeur et al. 2016) Trajectories and velocity profiles of horizontal movements
779 performed under normal, hyper, and micro-gravity. **(I)** Schematic top view of a participant
780 performing the task. **(J)** Mean and standard error of trajectories in the frontal plane from the point of
781 view of the subject. Traces correspond to rightward movements (n=10 participants). Gravity was
782 aligned with the direction $-Z$. **(K)** Velocity traces along the X -axis across gravitational conditions,
783 highlighting systematic changes following changes in gravity orthogonal to the movement direction.
784

785 **Figure 3**

786 Different environments implying different force fields on the body are used to investigate whole-
787 body goal-directed reaching. From left to right: 1g=normal terrestrial condition; Aqua=Subaquatic
788 condition when immersed in a standard wetsuit; AquaS=Subaquatic condition when immersed in a
789 prototypical wetsuit for space training, and 0g=episodes of microgravity during parabolic flights. Data
790 present the mean final angular position of trunk relative to vertical as a function of the environment
791 for whole body reaching movements toward far targets. Adapted from Macaluso et al., 2016; 2017.
792

793 **Figure 4**

794 Grip force adaptation across different gravitational environments. **(Upper row)** Grip force/Load force
795 modulation is disrupted during the first exposure (Parabola 1) as highlighted by a large variability and
796 poor linear correlation, except in the 1g condition (green line). Reorganization then occurs over time
797 and normalizes after the 5th parabola. **(Lower row)** Grip force versus Load force traces in a typical
798 subject across conditions of partial gravity corresponding to gravity on the Moon and on Mars. Light,
799 medium and dark traces correspond to early, middle and late trials, respectively (Adapted from
800 Augurelle et al., 2003 and Opsomer et al., 2018).

801

802 **Figure 5**

803 Schematic illustration of the combination of visual, vestibular, and somatosensory feedback in an
804 internal model (IM) of body and environmental dynamics used to estimate gravity (\hat{g}).
805 Somatosensory feedback conveys information about the weight of body segments and held objects
806 (W_i) through muscle and skin afferent feedback (left panel, black arrows). The estimate of gravity is
807 formed by combining the different feedback modalities according to the weights of body parts and of
808 the objects that we manipulate (W_i). This estimate is then used by a motor command generator (C)
809 that depends on \hat{g} . Multimodal and gravity-dependent inference about gravity may explain how
810 motor commands adapt quickly but only partially to the context.

811

812 **References**

- 813 **Adams WJ.** A common light-prior for visual search, shape, and reflectance judgments. *J Vis* , 2007.
814 doi:10.1167/7.11.11.
- 815 **Alberts BBGT, de Brouwer AJ, Selen LPJ, Medendorp WP.** A Bayesian account of visual-vestibular
816 interactions in the rod-and-frame task. *eNeuro* , 2016a. doi:10.1523/ENEURO.0093-16.2016.
- 817 **Alberts BBGT, Selen LPJ, Bertolini G, Straumann D, Medendorp WP, Tarnutzer AA.** Dissociating
818 vestibular and somatosensory contributions to spatial orientation. *J Neurophysiol* , 2016b.
819 doi:10.1152/jn.00056.2016.
- 820 **Angelaki DE, Dickman JD.** Spatiotemporal processing of linear acceleration: primary afferent and
821 central vestibular neuron responses. *J Neurophysiol* 84: 2113–2132, 2000.
- 822 **Angelaki DE, McHenry MQ, Dickman JD, Newlands SD, Hess BJ.** Computation of inertial motion:
823 neural strategies to resolve ambiguous otolith information. *J Neurosci* 19: 316–327, 1999.
- 824 **Angelaki DE, Shaikh AG, Green AM, Dickman JD.** Neurons compute internal models of the physical
825 laws of motion. *Nature* 430: 560–564, 2004.
- 826 **Atkeson CG, Hollerbach JM.** Kinematic features of unrestrained vertical arm movements. *J Neurosci*
827 5: 2318–30, 1985.
- 828 **Augurelle A-S, Penta M, White O, Thonnard J-L.** The effects of a change in gravity on the dynamics of
829 prehension. *Exp brain Res* 148: 533–40, 2003.
- 830 **Baier B, Vogt T, Rohde F, Cuvenhaus H, Conrad J, Dieterich M.** Deep brain stimulation of the nucleus
831 ventralis intermedius: a thalamic site of graviceptive modulation. *Brain Struct Funct* , 2017.
832 doi:10.1007/s00429-015-1157-x.
- 833 **Barbiero M, Rousseau C, Papaxanthis C, White O.** Coherent multimodal sensory information allows
834 switching between gravito-inertial contexts. *Front Physiol* 8: 290, 2017.
- 835 **Berret B, Bonnetblanc F, Papaxanthis C, Pozzo T.** Modular control of pointing beyond arm’s length. *J*
836 *Neurosci* 29: 191–205, 2009.
- 837 **Berret B, Chiovetto E, Nori F, Pozzo T.** Evidence for composite cost functions in arm movement
838 planning: An inverse optimal control approach. *PLoS Comput Biol* , 2011.
839 doi:10.1371/journal.pcbi.1002183.
- 840 **Berret B, Darlot C, Jean F, Pozzo T, Papaxanthis C, Gauthier JP.** The inactivation principle:
841 mathematical solutions minimizing the absolute work and biological implications for the planning of
842 arm movements. *PLoS Comput Biol* 4: e1000194, 2008.
- 843 **Berret B, Delis I, Gaveau J, Jean F.** Optimality and Modularity in Human Movement: From Optimal
844 Control to Muscle Synergies. In: *Biomechanics of Anthropomorphic Systems*, edited by Venture G,
845 Laumond J-P, Watier B. Springer International Publishing, p. 105–133.

846 **Bock O.** Problems of sensorimotor coordination in weightlessness. *Brain Res. Rev.* 28: 155–160, 1998.

847 **Boulanger N, Buisseret F, Dehouck V, Dierick F, White O.** Adiabatic invariants drive rhythmic human
848 motion in variable gravity. *bioRxiv* 674143, 2019.

849 **Bringoux L, Blouin J, Coyle T, Ruget H, Mouchnino L.** Effect of gravity-like torque on goal-directed
850 arm movements in microgravity. *J Neurophysiol* 107: 2541–2548, 2012a.

851 **Bringoux L, Lepecq J-C, Danion F.** Does visually induced self-motion affect grip force when holding an
852 object? *J Neurophysiol* 108: 1685–94, 2012b.

853 **Bringoux L, Nougier V, Barraud P-A, Marin L, Raphel C.** Contribution of somesthetic information to
854 the perception of body orientation in the pitch dimension. *Q J Exp Psychol A* 56: 909–923, 2003.

855 **Bringoux L, Scotto Di Cesare C, Borel L, Macaluso T, Sarlegna FR.** Do Visual and Vestibular Inputs
856 Compensate for Somatosensory Loss in the Perception of Spatial Orientation? Insights from a
857 Deafferented Patient. *Front Hum Neurosci* 10: 181, 2016.

858 **Brown J.** Orientation to the vertical during water immersion. *Aerosp Med* 32: 209–217, 1961.

859 **Bunn LM, Marsden JF, Voyce DC, Giunti P, Day BL.** Sensorimotor processing for balance in
860 spinocerebellar ataxia type 6. *Mov Disord* , 2015. doi:10.1002/mds.26227.

861 **Carriot J, Bringoux L, Charles C, Mars F, Nougier V, Cian C.** Perceived body orientation in
862 microgravity: effects of prior experience and pressure under the feet. *Aviat Space Environ Med* 75:
863 795–799, 2004.

864 **Casellato C, Tagliabue M, Pedrocchi A, Papaxanthis C, Ferrigno G, Pozzo T.** Reaching while standing
865 in microgravity: a new postural solution to oversimplify movement control. *Exp brain Res* 216: 203–
866 15, 2012.

867 **Cebolla AM, Petieau M, Dan B, Balazs L, McIntyre J, Cheron G.** Cerebellar contribution to visuo-
868 attentional alpha rhythm: Insights from weightlessness. *Sci Rep* , 2016. doi:10.1038/srep37824.

869 **Chang YH, Huang HW, Hamerski CM, Kram R.** The independent effects of gravity and inertia on
870 running mechanics. *J Exp Biol* 203: 229–238, 2000.

871 **Cheron G, Leroy a, De Saedeleer C, Bengoetxea a, Lipshits M, Cebolla a, Servais L, Dan B, Berthoz
872 a, McIntyre J.** Effect of gravity on human spontaneous 10-Hz electroencephalographic oscillations
873 during the arrest reaction. *Brain Res* 1121: 104–16, 2006.

874 **Cheron G, Leroy A, Palmero-Soler E, De Saedeleer C, Bengoetxea A, Cebolla A-MM, Vidal M, Dan B,
875 Berthoz A, McIntyre J.** Gravity influences top-down signals in visual processing. *PLoS One* 9: e82371,
876 2014.

877 **Claassen J, Bardins S, Spiegel R, Strupp M, Kalla R.** Gravity matters: Motion perceptions modified by
878 direction and body position. *Brain Cogn* , 2016. doi:10.1016/j.bandc.2016.05.003.

879 **Clemens IAH, de Vrijer M, Selen LPJ, van Gisbergen JAM, Medendorp WP.** Multisensory processing
880 in spatial orientation: An inverse probabilistic approach. *J Neurosci* , 2011.

881 doi:10.1523/JNEUROSCI.6472-10.2011.

882 **Clément G, Arnesen TN, Olsen MH, Sylvestre B.** Perception of longitudinal body axis in microgravity
883 during parabolic flight. *Neurosci Lett* 413: 150–153, 2007.

884 **Cluff T, Crevecoeur F, Scott SH.** A perspective on multisensory integration and rapid perturbation
885 responses. *Vision Res*, 2015. doi:10.1016/j.visres.2014.06.011.

886 **Cole KJ, Johansson RS.** Friction at the digit-object interface scales the sensorimotor transformation
887 for grip responses to pulling loads. *Exp Brain Res* 95: 523–532, 1993.

888 **Crevecoeur F, Kurtzer I.** Long-latency reflexes for inter-effector coordination reflect a continuous
889 state feedback controller. *J Neurophysiol*, 2018. doi:10.1152/jn.00205.2018.

890 **Crevecoeur F, McIntyre J, Thonnard J-L, Lefèvre P.** Gravity-dependent estimates of object mass
891 underlie the generation of motor commands for horizontal limb movements. *J Neurophysiol* 384–392,
892 2014.

893 **Crevecoeur F, McIntyre J, Thonnard JL, Lefèvre P.** Movement stability under uncertain internal
894 models of dynamics. *J Neurophysiol*, 2010a. doi:10.1152/jn.00315.2010.

895 **Crevecoeur F, Munoz DP, Scott SH.** Dynamic Multisensory integration: Somatosensory speed Trumps
896 Visual accuracy during feedback control. *J Neurosci*, 2016. doi:10.1523/JNEUROSCI.0184-16.2016.

897 **Crevecoeur F, Sepulchre RJ, Thonnard JL, Lefèvre P.** Improving the state estimation for optimal
898 control of stochastic processes subject to multiplicative noise. *Automatica*, 2011.
899 doi:10.1016/j.automatica.2011.01.026.

900 **Crevecoeur F, Thonnard J-L, Lefèvre P.** Optimal integration of gravity in trajectory planning of
901 vertical pointing movements. *J Neurophysiol* 102: 786–96, 2009a.

902 **Crevecoeur F, Thonnard J-L, Lefèvre P.** Sensorimotor Mapping for Anticipatory Grip Force
903 Modulation. *J Neurophysiol*, 2010b. doi:10.1152/jn.00114.2010.

904 **Crevecoeur F, Thonnard JL, Lefèvre P.** Forward models of inertial loads in weightlessness.
905 *Neuroscience* 161: 589–98, 2009b.

906 **Cutfield NJ, Scott G, Waldman AD, Sharp DJ, Bronstein AM.** Visual and proprioceptive interaction in
907 patients with bilateral vestibular loss. *NeuroImage Clin*, 2014. doi:10.1016/j.nicl.2013.12.013.

908 **Dakin CJ, Peters A, Giunti P, Day BL.** Cerebellar Degeneration Increases Visual Influence on Dynamic
909 Estimates of Verticality. *Curr Biol*, 2018. doi:10.1016/j.cub.2018.09.049.

910 **Dakin CJ, Rosenberg A.** Chapter 3 - Gravity estimation and verticality perception. In: *Balance, Gait,*
911 *and Falls*, edited by Day BL, Lord SR. Elsevier, p. 43–59. 2018.

912 **Dalecki M, Dräger T, Mierau a, Bock O.** Production of finely graded forces in humans: effects of
913 simulated weightlessness by water immersion. *Exp brain Res* 218: 41–7, 2012.

914 **Demertzi A, van Ombergen A, Tomilovskaya E, Jeurissen B, Pechenkova E, Di Perri C, Litvinova L,**
915 **Amico E, Rumshiskaya A, Rukavishnikov I, Sijbers J, Sinitsyn V, Kozlovskaya IB, Sunaert S, Parizel**

916 **PM, van de Heyning PH, Laureys S, Wuyts FL.** Cortical reorganization in an astronaut's brain after
917 long-duration spaceflight. *Brain Struct Funct* 1, 2016.

918 **DiZio P, Lackner JR.** Sensorimotor aspects of high-speed artificial gravity III: Sensorimotor adaptation.
919 *J Vestib Res Equilib Orientat* 12: 291–299, 2002.

920 **Dokka K, DeAngelis GC, Angelaki DE.** Multisensory Integration of Visual and Vestibular Signals
921 Improves Heading Discrimination in the Presence of a Moving Object. *J Neurosci* , 2015.
922 doi:10.1523/JNEUROSCI.2267-15.2015.

923 **Dyde RT, Jenkin MR, Jenkin HL, Zacher JE, Harris LR.** The effect of altered gravity states on the
924 perception of orientation. *Exp Brain Res* 194: 647–660, 2009.

925 **Flanagan JR, Wing AM.** The stability of precision grip forces during cyclic arm movements with a
926 hand-held load. *Exp Brain Res* 105: 455–464, 1995.

927 **Flanagan JR, Wing AM.** The role of internal models in motion planning and control: evidence from
928 grip force adjustments during movements of hand-held loads. *J Neurosci* 17: 1519–1528, 1997.

929 **Flanders M, Herrmann U.** Two components of muscle activation: scaling with the speed of arm
930 movement. *J Neurophysiol* , 1992. doi:10.1152/jn.1992.67.4.931.

931 **Foxe JJ, Snyder AC.** The role of alpha-band brain oscillations as a sensory suppression mechanism
932 during selective attention. *Front Psychol* , 2011. doi:10.3389/fpsyg.2011.00154.

933 **Gallagher M, Ferrè ER.** The aesthetics of verticality: A gravitational contribution to aesthetic
934 preference. *Q J Exp Psychol* , 2018. doi:10.1177/1747021817751353.

935 **Gaveau J, Berret B, Angelaki DE, Papaxanthis C.** Direction-dependent arm kinematics reveal optimal
936 integration of gravity cues. *Elife* 5: e16394, 2016.

937 **Gaveau J, Berret B, Demougeot L, Fadiga L, Pozzo T, Papaxanthis C.** Energy-related optimal control
938 accounts for gravitational load: comparing shoulder, elbow, and wrist rotations. *J Neurophysiol* 111:
939 4–16, 2014.

940 **Gaveau J, Paizis C, Berret B, Pozzo T, Papaxanthis C.** Sensorimotor adaptation of point-to-point arm
941 movements after spaceflight: the role of internal representation of gravity force in trajectory
942 planning. *J Neurophysiol* 106: 620–629, 2011.

943 **Gaveau J, Papaxanthis C.** The temporal structure of vertical arm movements. *PLoS One* 6: e22045,
944 2011.

945 **Gentili R, Cahouet V, Papaxanthis C.** Motor planning of arm movements is direction-dependent in
946 the gravity field. *Neuroscience* 145: 20–32, 2007.

947 **Giard T, Crevecoeur F, McIntyre J, Thonnard JL, Lefèvre P.** Inertial torque during reaching directly
948 impacts grip-force adaptation to weightless objects. *Exp Brain Res* , 2015. doi:10.1007/s00221-015-
949 4400-z.

950 **Glasauer S, Mittelstaedt H.** Determinants of orientation in microgravity. *Acta Astronaut* , 1992.

951 doi:10.1016/0094-5765(92)90167-H.

952 **Göbel S, Bock O, Pongratz H, Krause W.** Practice ameliorates deficits of isometric force production in
953 +3 Gz. *Aviat Sp Environ Med* 77: 586–591, 2006.

954 **Gravano S, Zago M, Lacquaniti F.** Mental imagery of gravitational motion. *Cortex*, 2017.
955 doi:10.1016/j.cortex.2017.08.005.

956 **Hermsdörfer J, Marquardt C, Philipp J, Zierdt A, Nowak D, Glasauer S, Mai N.** Grip forces exerted
957 against stationary held objects during gravity changes. *Exp Brain Res* 126: 205–214, 1999.

958 **Hollerbach JM, Flash T.** Dynamic interactions between limb segments during planar arm movement.
959 *Biol Cybern* , 1982. doi:10.1007/BF00353957.

960 **Indovina I, Maffei V, Bosco G, Zago M, Macaluso E, Lacquaniti F.** Representation of visual
961 gravitational motion in the human vestibular cortex. *Science* 308: 416–419, 2005.

962 **Izawa J, Rane T, Donchin O, Shadmehr R.** Motor adaptation as a process of reoptimization. *J*
963 *Neurosci* 28: 2883–2891, 2008.

964 **Jahn K, Deutschländer A, Stephan T, Strupp M, Wiesmann M, Brandt T.** Brain activation patterns
965 during imagined stance and locomotion in functional magnetic resonance imaging. *Neuroimage* 22:
966 1722–1731, 2004.

967 **Jenkin MR, Dyde RT, Jenkin HL, Zacher JE, Harris LR.** Perceptual upright: the relative effectiveness of
968 dynamic and static images under different gravity States. *Seeing Perceiving* 24: 53–64, 2011.

969 **Jörges B, López-Moliner J.** Gravity as a Strong Prior: Implications for Perception and Action. *Front*
970 *Hum Neurosci* 11, 2017.

971 **Karim HT, Sparto PJ, Aizenstein HJ, Furman JM, Huppert TJ, Erickson KI, Loughlin PJ.** Functional MR
972 imaging of a simulated balance task. *Brain Res* 1555: 20–27, 2014.

973 **Kawato M.** Internal models for motor control and trajectory planning. *Curr. Opin. Neurobiol.* 9: 718–
974 727, 1999.

975 **Kheradmand A, Otero-Millan J.** Spatial orientation: Model-based approach to multi-sensory
976 mechanisms. In: *Progress in Brain Research*. 2019.

977 **Kheradmand A, Winnick A.** Perception of upright: Multisensory convergence and the role of
978 temporo-parietal cortex. *Front Neurol* , 2017. doi:10.3389/fneur.2017.00552.

979 **Koppelmans V, Scott JM, Downs ME, Cassady KE, Yuan P, Pasternak O, Wood SJ, De Dios YE, Gadd**
980 **NE, Kofman I, Riascos R, Reuter-Lorenz PA, Bloomberg JJ, Mulavara AP, Ploutz-Snyder LL, Seidler RD.**
981 Exercise effects on bed rest-induced brain changes. *PLoS One* , 2018.
982 doi:10.1371/journal.pone.0205515.

983 **Kornilova LN, Mueller C, Wiest G, Shtenvender G, Toyer R, Chernobyl'skiĭ LM, Smirnov VA, Poliakov**
984 **A V.** [Awareness of the subjective vertical in weightlessness (results of Austrian-Russian experiment
985 Optovert performed within the framework of the program Austromir, part III)]. *Aviakosm Ekolog Med*

986 30: 11–15, 1996.

987 **Krafczyk S, Knappek M, Philipp J, Querner V, Dieterich M.** Optokinetic stimulation in microgravity:
988 torsional eye movements and subjective visual vertical. *Aviat Space Environ Med* 74: 517–521, 2003.

989 **Kremmyda O, Kirsch V, Bardins S, Lohr H, Vollmar C, Noachtar S, Dieterich M.** Electrical brain
990 stimulation of the parietal lobe impairs the perception of verticality. *J. Neurol.* 2019.

991 **Lackner JR, Dizio P.** Rapid adaptation to Coriolis force perturbations of arm trajectory. *J Neurophysiol*
992 72: 299–313, 1994.

993 **Lackner JR, Dizio P.** Angular displacement perception modulated by force background. *Exp Brain Res* ,
994 2009. doi:10.1007/s00221-009-1785-6.

995 **Lackner JR, DiZio P.** Multisensory, cognitive, and motor influences on human spatial orientation in
996 weightlessness. *J Vestib Res Equilib Orientat* 3: 361–372, 1993.

997 **Lackner JR, DiZio P.** Human orientation and movement control in weightless and artificial gravity
998 environments. *Exp Brain Res* 130: 2–26, 2000a.

999 **Lackner JR, DiZio P.** Vestibular, Proprioceptive, and Haptic Contributions to Spatial Orientation. *Annu*
1000 *Rev Psychol* , 2005. doi:10.1146/annurev.psych.55.090902.142023.

1001 **Lackner JR, DiZio P.** Dynamic Sensory-Motor Adaptation to Earth Gravity. In: *Sensation, Perception,*
1002 *and Attention.* New York: Wiley, 2018, p. 887–906.

1003 **Lackner JR, DiZio PA.** Aspects of body self-calibration. *Trends Cogn. Sci.* 2000b.

1004 **Lacquaniti F, Bosco G, Gravano S, Indovina I, La Scaleia B, Maffei V, Zago M.** Multisensory
1005 integration and internal models for sensing gravity effects in primates. *Biomed Res. Int.* 2014.

1006 **Lacquaniti F, Bosco G, Gravano S, Indovina I, La Scaleia B, Maffei V, Zago M.** Gravity in the brain as a
1007 reference for space and time perception. *Multisens. Res.* 2015.

1008 **Lacquaniti F, Bosco G, Indovina I, La Scaleia B, Maffei V, Moscatelli A, Zago M.** Visual gravitational
1009 motion and the vestibular system in humans. *Front Integr Neurosci* , 2013.
1010 doi:10.3389/fnint.2013.00101.

1011 **Lacquaniti F, Maioli C.** The role of preparation in tuning anticipatory and reflex responses during
1012 catching. [Online]. *J Neurosci* 9: 134–48, 1989<http://www.ncbi.nlm.nih.gov/pubmed/2913200>.

1013 **Langolf GD, Chaffin DB, Foulke JA.** An investigation of fitts' law using a wide range of movement
1014 amplitudes. *J Mot Behav* , 1976. doi:10.1080/00222895.1976.10735061.

1015 **Lathan C, Wang Z, Clément G.** Changes in the vertical size of a three-dimensional object drawn in
1016 weightlessness by astronauts. [Online]. *Neurosci Lett* 295: 37–40,
1017 2000<http://www.ncbi.nlm.nih.gov/pubmed/11078931>.

1018 **Laurens J, Kim B, Dickman JD, Angelaki DE.** Gravity orientation tuning in macaque anterior thalamus.
1019 *Nat. Neurosci.* 2016.

1020 **Laurens J, Meng H, Angelaki DE.** Computation of linear acceleration through an internal model in the

1021 macaque cerebellum. *Nat Neurosci* , 2013a. doi:10.1038/nn.3530.

1022 **Laurens J, Meng H, Angelaki DE.** Neural representation of orientation relative to gravity in the
1023 macaque cerebellum. *Neuron* , 2013b. doi:10.1016/j.neuron.2013.09.029.

1024 **Lee JK, Koppelmans V, Riascos RF, Hasan KM, Pasternak O, Mulavara AP, Bloomberg JJ, Seidler RD.**
1025 Spaceflight-Associated Brain White Matter Microstructural Changes and Intracranial Fluid
1026 Redistribution. In: *JAMA Neurology*. 2019.

1027 **Lopez C, Blanke O, Mast FW.** The human vestibular cortex revealed by coordinate-based activation
1028 likelihood estimation meta-analysis. *Neuroscience* , 2012. doi:10.1016/j.neuroscience.2012.03.028.

1029 **Lucertini M, De Angelis C, Martelli M, Zolesi V, Tomao E.** Subjective visual vertical in erect/supine
1030 subjects and under microgravity: effects of lower body negative pressure. *Eur Arch oto-rhino-*
1031 *laryngology Off J Eur Fed Oto-Rhino-Laryngological Soc Affil with Ger Soc Oto-Rhino-Laryngology -*
1032 *Head Neck Surg* 268: 1067–1075, 2011.

1033 **Macaluso T, Bourdin C, Buloup F, Mille M-L, Sainton P, Sarlegna FR, Taillebot V, Vercher J-L, Weiss P,**
1034 **Bringoux L.** Kinematic features of whole-body reaching movements underwater: Neutral buoyancy
1035 effects. *Neuroscience Epub Ahead*: 125–135, 2016.

1036 **Macaluso T, Bourdin C, Buloup F, Mille ML, Sainton P, Sarlegna FR, Vercher JL, Bringoux L.**
1037 Sensorimotor reorganizations of arm kinematics and postural strategy for functional whole-body
1038 reaching movements in microgravity. *Front Physiol* , 2017. doi:10.3389/fphys.2017.00821.

1039 **MacNeilage PR, Glasauer S.** Gravity Perception: The Role of the Cerebellum. *Curr Biol* 28: R1296–
1040 R1298, 2018.

1041 **Maffei V, Mazzarella E, Piras F, Spalletta G, Caltagirone C, Lacquaniti F, Daprati E.** Processing of
1042 visual gravitational motion in the peri-sylvian cortex: Evidence from brain-damaged patients. *Cortex* ,
1043 2016. doi:10.1016/j.cortex.2016.02.004.

1044 **Malouin F, Richards CL, Jackson PL, Dumas F, Doyon J.** Brain activations during motor imagery of
1045 locomotor-related tasks: A PET study. *Hum Brain Mapp* 19: 47–62, 2003.

1046 **Massion J, Fabre JC, Mouchnino L, Obadia A.** Body orientation and regulation of the center of gravity
1047 during movement under water. *J Vestib Res Equilib Orientat* 5: 211–221, 1995.

1048 **McIntyre J, Berthoz A, Lacquaniti F.** Reference frames and internal models for visuo-manual
1049 coordination: what can we learn from microgravity experiments? *Brain Res Brain Res Rev* 28: 143–54,
1050 1998.

1051 **Mcintyre J, Zago M, Berthoz A, Lacquaniti F.** Does the brain model Newton ' s laws ? 4: 693–694,
1052 2001.

1053 **Mechtcheriakov S, Berger M, Molokanova E, Holzmueller G, Wirtenberger W, Lechner-Steinleitner**
1054 **S, De Col C, Kozlovskaya I, Gerstenbrand F.** Slowing of human arm movements during
1055 weightlessness: The role of vision. *Eur J Appl Physiol* 87: 576–583, 2002.

1056 **Medendorp WP, Alberts BBGT, Verhagen WIM, Koppen M, Selen LPJ.** Psychophysical evaluation of
1057 sensory reweighting in bilateral vestibulopathy. *Front. Neurol.* 2018.

1058 **Merfeld DM, Zupan L, Peterka RJ.** Humans use internal models to estimate gravity and linear
1059 acceleration. *Nature* , 1999. doi:10.1038/19303.

1060 **Mergner T, Huber W, Becker W.** Vestibular-neck interaction and transformation of sensory
1061 coordinates. *J Vestib Res Orientat* , 1997.

1062 **Mierau A, Girgenrath M, Bock O.** Isometric force production during changed-Gz episodes of
1063 parabolic flight. *Eur J Appl Physiol* 102: 313–8, 2008.

1064 **Miller WL, Maffei V, Bosco G, Iosa M, Zago M, Macaluso E, Lacquaniti F.** Vestibular nuclei and
1065 cerebellum put visual gravitational motion in context. *J Neurophysiol* 99: 1969–1982, 2008.

1066 **Mittelstaedt H.** A new solution to the problem of the subjective vertical. *Naturwissenschaften* , 1983.
1067 doi:10.1007/BF00404833.

1068 **Nelson JG.** Effect of water immersion and body position upon perception of the gravitational vertical.
1069 *Aerosp Med* , 1968.

1070 **Nowak DA, Hermsdörfer J, Philipp J, Marquardt C, Glasauer S, Mai N.** Effects of changing gravity on
1071 anticipatory grip force control during point-to-point movements of a hand-held object. *Motor Control*
1072 5: 231–253, 2001.

1073 **Nowak ZD, Hermsdörfer J, Marquardt C, Philipp J, Zierdt A, Nowak D, Glasauer S, Mai N, Nowak ZD.**
1074 Moving weightless objects. Grip force control during microgravity. *Exp Brain Res* 132: 52–64, 2000.

1075 **Oostwoud Wijdenes L, Medendorp WP.** State Estimation for Early Feedback Responses in Reaching:
1076 Intramodal or Multimodal? *Front Integr Neurosci* 11: 1–8, 2017.

1077 **Opsomer L, Théate V, Lefèvre P, Thonnard JL.** Dexterous manipulation during rhythmic arm
1078 movements in Mars, Moon, and micro-gravity. *Front Physiol* 9, 2018.

1079 **Papaxanthis C, Dubost V, Pozzo T.** Similar planning strategies for whole-body and arm movements
1080 performed in the sagittal plane. *Neuroscience* 117: 779–783, 2003.

1081 **Papaxanthis C, Pozzo T, Intyre JMC, McIntyre J.** Kinematic and dynamic processes for the control of
1082 pointing movements in humans revealed by short-term exposure to microgravity. *Neuroscience* 135:
1083 371–383, 2005.

1084 **Papaxanthis C, Pozzo T, McIntyre J.** Arm end-point trajectories under normal and micro-gravity
1085 environments. *Acta Astronaut* 43: 153–161, 1998a.

1086 **Papaxanthis C, Pozzo T, Popov KE, McIntyre J.** Hand trajectories of vertical arm movements in one-G
1087 and zero-G environments. Evidence for a central representation of gravitational force. *Exp Brain Res*
1088 120: 496–502, 1998b.

1089 **Papaxanthis C, Pozzo T, Stapley P.** Effects of movement direction upon kinematic characteristics of
1090 vertical arm pointing movements in man. 253: 103–106, 1998c.

1091 **Pletser V, Winter J, Duclos F, Bret-Dibat T, Friedrich U, Clervoy JF, Gharib T, Gai F, Minster O,**
1092 **Sundblad P.** The first joint european partial-G parabolic flight campaign at moon and mars gravity
1093 levels for science and exploration. *Microgravity Sci Technol* , 2012. doi:10.1007/s12217-012-9304-y.
1094 **Pozzo T, Papaxanthis C, Stapley P, Berthoz A.** The sensorimotor and cognitive integration of gravity.
1095 *Brain Res Brain Res Rev* 28: 92–101, 1998.
1096 **Riascos RF, Kamali A, Hakimelahi R, Mwangi B, Rabiei P, Seidler RD, Behzad BB, Keser Z, Kramer LA,**
1097 **Hasan KM.** Longitudinal Analysis of Quantitative Brain MRI in Astronauts Following Microgravity
1098 Exposure. *J Neuroimaging* , 2019. doi:10.1111/jon.12609.
1099 **Ross HE.** Orientation and movement in divers. In: *Perception control of self-motion*. In R. Warren & A.
1100 H. Wertheim (Eds.), 1990, p. 463–486.
1101 **Rousseau C, Barbiero M, Pozzo T, Papaxanthis C, White O.** Gravity highlights a dual role of the insula
1102 in internal models. *bioRxiv* 17–19, 2019.
1103 **Rousseau C, Fautrelle L, Papaxanthis C, Fadiga L, Pozzo T, White O.** Direction-dependent activation
1104 of the insular cortex during vertical and horizontal hand movements. *Neuroscience* 325: 10–19,
1105 2016a.
1106 **Rousseau C, Papaxanthis C, Gaveau J, Pozzo T, White O.** Initial information prior to movement onset
1107 influences kinematics of upward arm pointing movements. *J Neurophysiol* 116: jn.00616.2015, 2016b.
1108 **La Scaleia B, Lacquaniti F, Zago M.** Body orientation contributes to modelling the effects of gravity
1109 for target interception in humans. *J Physiol* , 2019. doi:10.1113/JP277469.
1110 **La Scaleia B, Zago M, Lacquaniti F.** Hand interception of occluded motion in humans: A test of
1111 model-based vs.on-line control. *J Neurophysiol* , 2015. doi:10.1152/jn.00475.2015.
1112 **Schaal S, Sternad D, Osu R, Kawato M.** Rhythmic arm movement is not discrete. 7: 1137–1144, 2004.
1113 **Sciutti A, Demougeot L, Berret B, Toma S, Sandini G, Papaxanthis C, Pozzo T.** Visual gravity
1114 influences arm movement planning. *J Neurophysiol* 107: 3433–45, 2012.
1115 **Scott SH.** A Functional Taxonomy of Bottom-Up Sensory Feedback Processing for Motor Actions.
1116 *Trends Neurosci.* 2016.
1117 **Le Seac’h AB, McIntyre J.** Multimodal reference frame for the planning of vertical arms movements.
1118 *Neurosci Lett* 423: 211–5, 2007.
1119 **Senot P.** Anticipating the Effects of Gravity When Intercepting Moving Objects: Differentiating Up
1120 and Down Based on Nonvisual Cues. *J Neurophysiol* , 2005. doi:10.1152/jn.00527.2005.
1121 **Senot P, Zago M, Lacquaniti F, McIntyre J.** Anticipating the Effects of Gravity When Intercepting
1122 Moving Objects : Differentiating Up and Down Based on Nonvisual Cues Anticipating the Effects of
1123 Gravity When Intercepting Moving Objects : Differentiating Up and Down Based on Nonvisual Cues.
1124 4471–4480, 2005.
1125 **Senot P, Zago M, Le Séac’h A, Zaoui M, Berthoz A, Lacquaniti F, McIntyre J, Le Seac’h A, Zaoui M,**

1126 **Berthoz A, Lacquaniti F, McIntyre J, Le Séac'h A, Zaoui M, Berthoz A, Lacquaniti F, McIntyre J, Le**
1127 **Seac'h A, Zaoui M, Berthoz A, Lacquaniti F, McIntyre J.** When Up Is Down in Og: How Gravity Sensing
1128 Affects the Timing of Interceptive Actions. *J Neurosci* 32: 1969–73, 2012.

1129 **Shadmehr R, Mussa-Ivaldi F.** Adaptive representation of dynamics during learning of a motor task. *J*
1130 *Neurosci* 14, 3208-3224 , 1994.

1131 **Shadmehr R, Smith MA, Krakauer JW.** Error Correction, Sensory Prediction, and Adaptation in Motor
1132 Control. *Annu Rev Neurosci* , 2010. doi:10.1146/annurev-neuro-060909-153135.

1133 **Shelhamer M.** Parabolic flight as a spaceflight analog. *J. Appl. Physiol.* 2016.

1134 **Soechting JF.** Effect of target size on spatial and temporal characteristics of a pointing movement in
1135 man. *Exp Brain Res* , 1984. doi:10.1007/BF00235824.

1136 **Tagliabue M, McIntyre J.** Necessity is the Mother of Invention: Reconstructing Missing Sensory
1137 Information in Multiple, Concurrent Reference Frames for Eye-Hand Coordination. *J Neurosci* , 2011.
1138 doi:10.1523/jneurosci.0623-10.2011.

1139 **Tagliabue M, McIntyre J.** A modular theory of multisensory integration for motor control. *Front*
1140 *Comput Neurosci* , 2014. doi:10.3389/fncom.2014.00001.

1141 **Tajadura-Jiménez A, Deroy O, Marquardt T, Bianchi-Berthouze N, Asai T, Kimura T, Kitagawa N.**
1142 Audio-tactile cues from an object's fall change estimates of one's body height. *PLoS One* , 2018.
1143 doi:10.1371/journal.pone.0199354.

1144 **Tarnutzer AA, Marti S, Straumann D.** Gravity perception in cerebellar patients. *Prog. Brain Res.* 2008.

1145 **Todorov E.** Optimality principles in sensorimotor control. *Nat Neurosci* 7: 907–15, 2004.

1146 **Wang W, Dounskaia N.** Neural control of arm movements reveals a tendency to use gravity to
1147 simplify joint coordination rather than to decrease muscle effort. *Neuroscience* , 2016.
1148 doi:10.1016/j.neuroscience.2016.10.009.

1149 **White O.** The brain adjusts grip forces differently according to gravity and inertia : a parabolic flight
1150 experiment. *Front Integr Neurosci* 9: 1–10, 2015.

1151 **White O, Barbiero M, Goswami N.** The effects of varying gravito-inertial stressors on grip strength
1152 and hemodynamic responses in men and women. *Eur J Appl Physiol* , 2019. doi:10.1007/s00421-019-
1153 04084-y.

1154 **White O, Bleyenheuft Y, Ronsse R, Smith AMAM, Thonnard J-LJ-L, Lefèvre P.** Altered gravity
1155 highlights central pattern generator mechanisms. *J Neurophysiol* 100: 2819–24, 2008a.

1156 **White O, Clément G, Fortrat J-O, Pavy-LeTraon A, Thonnard J-L, Blanc S, Wuyts FL, Paloski WH.**
1157 Towards human exploration of space: the THESEUS review series on neurophysiology research
1158 priorities. *npj Microgravity* 2: 16023, 2016.

1159 **White O, Dowling N, Bracewell RMM, Diedrichsen J.** Hand interactions in rapid grip force
1160 adjustments are independent of object dynamics. *J Neurophysiol* 100: 2738–45, 2008b.

1161 **White O, Lefèvre P, Wing AMAM, Bracewell RMM, Thonnard J-LJL.** Active Collisions in Altered
1162 Gravity Reveal Eye-Hand Coordination Strategies. *PLoS One* 7, 2012.

1163 **White O, McIntyre J, Augurelle A-SA-SS, Thonnard J-LJ-LL, McIntyre J.** Do novel gravitational
1164 environments alter the grip-force/load-force coupling at the fingertips? *Exp Brain Res* 163: 324–334,
1165 2005.

1166 **White O, Thonnard J-L, Lefèvre P, Hermsdörfer J.** Grip force adjustments reflect prediction of
1167 dynamic consequences in varying gravitoinertial fields. *Front Physiol* 9, 2018.

1168 **White O, Thonnard J-LJ-L, Wing AMM, Bracewell RMM, Diedrichsen J, Lefèvre P.** Grip force
1169 regulates hand impedance to optimize object stability in high impact loads. *Neuroscience* 189: 269–
1170 76, 2011.

1171 **de Winkel KN, Clément G, Groen EL, Werkhoven PJ.** The perception of verticality in lunar and
1172 Martian gravity conditions. *Neurosci Lett* 529: 7–11, 2012.

1173 **Wolpert DM, Diedrichsen J, Flanagan JR.** Principles of sensorimotor learning. *Nat Rev Neurosci* 12:
1174 739–51, 2011.

1175 **Yamamoto S, Kushiuro K.** Direction-dependent differences in temporal kinematics for vertical
1176 prehension movements. *Exp Brain Res* , 2014. doi:10.1007/s00221-013-3783-y.

1177 **Zago M, Bosco G, Maffei V, Iosa M, Ivanenko YP, Lacquaniti F.** Internal Models of Target Motion:
1178 Expected Dynamics Overrides Measured Kinematics in Timing Manual Interceptions. *J Neurophysiol*
1179 91: 1620–1634, 2004.

1180 **Zago M, Lacquaniti F.** Cognitive , perceptual and action-oriented representations of falling objects.
1181 43: 178–188, 2005a.

1182 **Zago M, Lacquaniti F.** Visual perception and interception of falling objects : a review of evidence for
1183 an internal model of gravity. 2, 2005b.

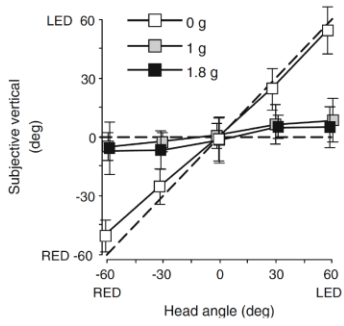
1184 **Zago M, Lacquaniti F.** Internal model of gravity for hand interception: Parametric adaptation to zero-
1185 gravity visual targets on Earth. *J Neurophysiol* 94: 1346–1357, 2005c.

1186 **Zago M, Lacquaniti F.** Compensation for time delays is better achieved in time than in space. *Behav*
1187 *Brain Sci* 31: 221–222, 2008.

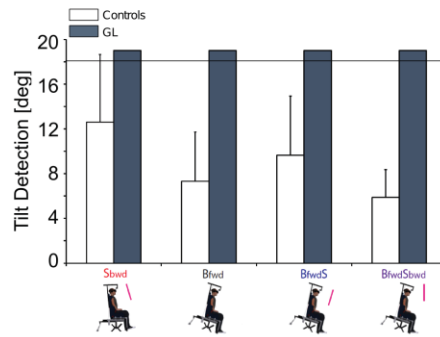
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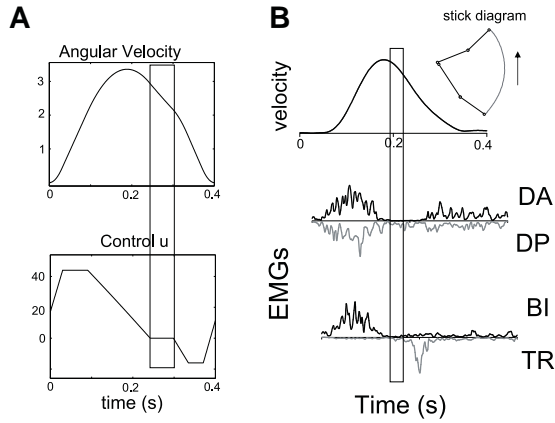
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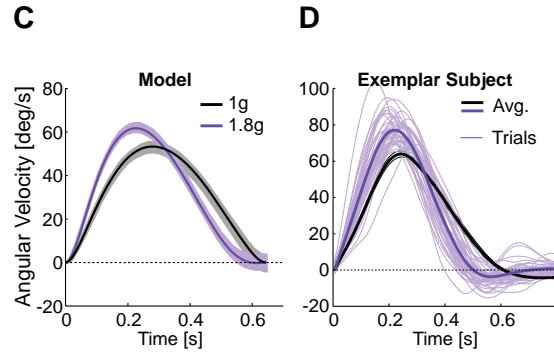
Bringoux et al., 2016:



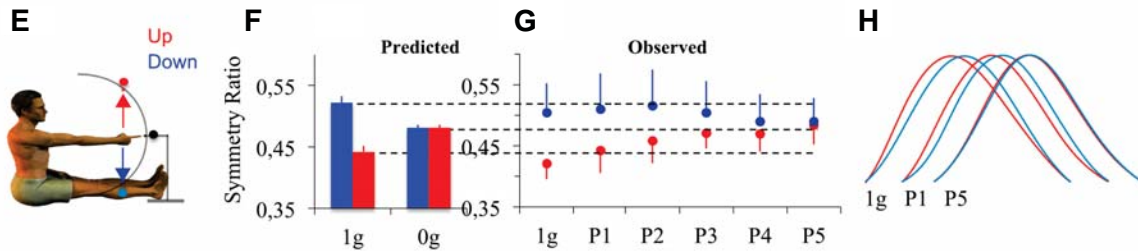
Berret et al., 2008



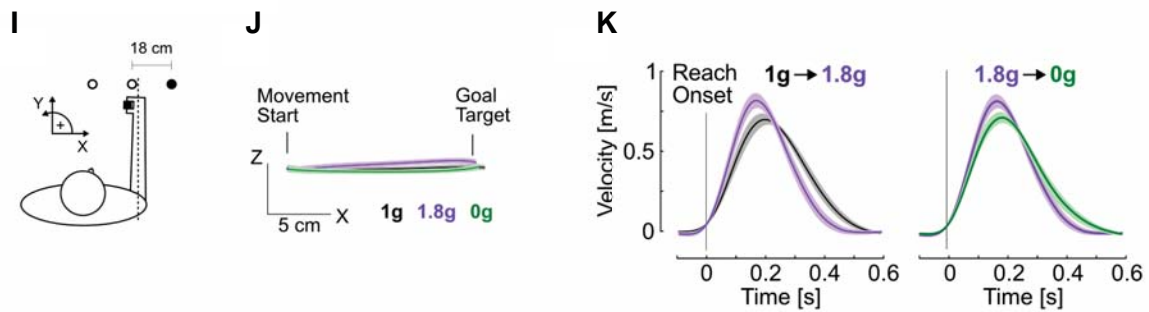
Crevecoeur et al., 2009

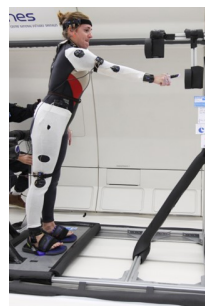
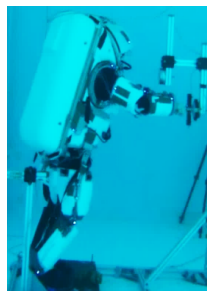
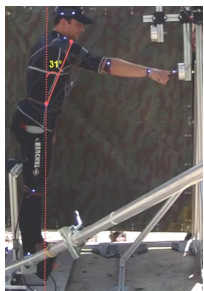
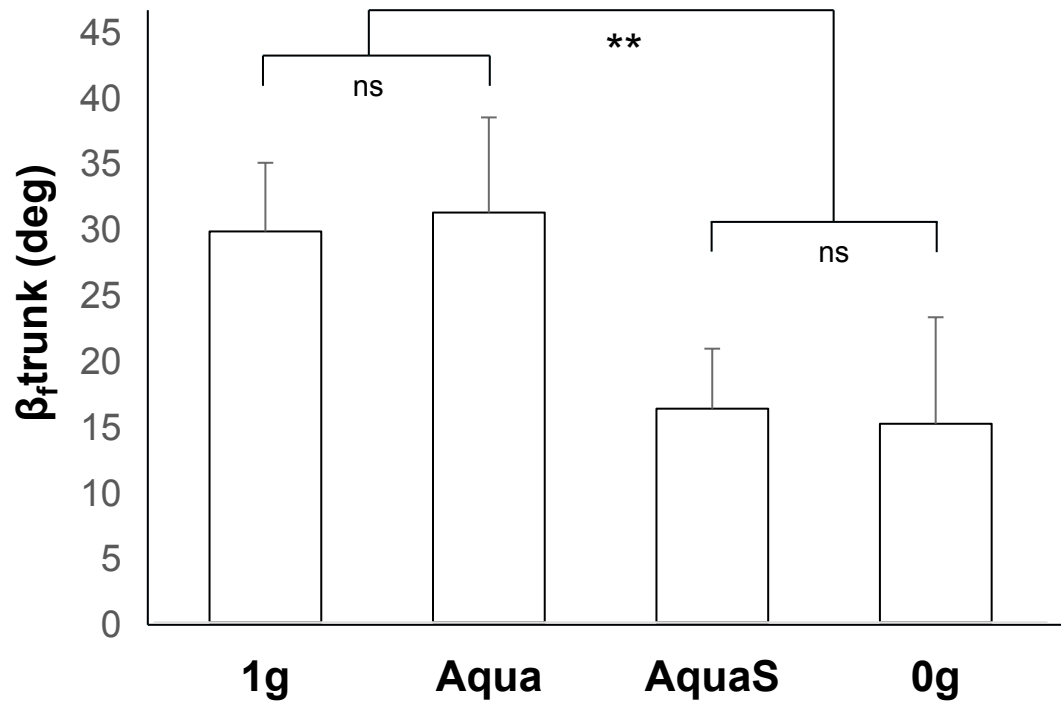


Gaveau et al., 2016

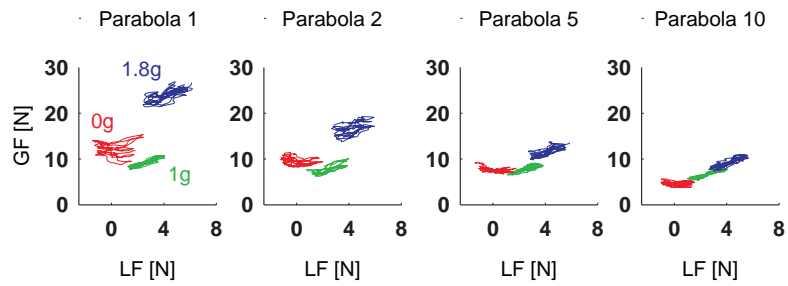


Crevecoeur et al., 2014





Augurelle et al., 2003



Opsomer et al., 2018

