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REVIEW | *Control of Movement*

The gravitational imprint on sensorimotor planning and control

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White O, Gaveau J, Bringoux L, Crevecoeur F. The gravitational imprint on sensorimotor planning and control. *J Neurophysiol* 124: 4–19, 2020. First published April 29, 2020; doi:10.1152/jn.00381.2019.—Humans excel at learning complex tasks, and elite performers such as musicians or athletes develop motor skills that defy biomechanical constraints. All actions require the movement of massive bodies. Of particular interest in the process of sensorimotor learning and control is the impact of gravitational forces on the body. Indeed, efficient control and accurate internal representations of the body configuration in space depend on our ability to feel and anticipate the action of gravity. Here we review studies on perception and sensorimotor control in both normal and altered gravity. Behavioral and modeling studies together suggested that the nervous system develops efficient strategies to take advantage of gravitational forces across a wide variety of tasks. However, when the body was exposed to altered gravity, the rate and amount of adaptation exhibited substantial variation from one experiment to another and sometimes led to partial adjustment only. Overall, these results support the hypothesis that the brain uses a multimodal and flexible representation of the effect of gravity on our body and movements. Future work is necessary to better characterize the nature of this internal representation and the extent to which it can adapt to novel contexts.

graviception; motor control; perception

INTRODUCTION

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

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

Although the hypothesis of a central representation of gravity has long been exploited in the field, it is important to recall that earlier work on the impact of gravity was shown to be inconclusive, owing to the large number of factors that differed

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across experiments (Bock 1998). It was argued in this earlier review that studies of sensorimotor coordination in space should carefully consider a number of confounding factors related to task dependency, sample size, and context, which were possible sources of discrepancies across collected results. The difficulty of gathering information due to the diversity and extreme nature of testing environments remains. However, since the review of O. Bock, converging evidence has emerged. Indeed, we now have at hand a larger number of studies performed in a broader range of testing conditions and performed in more constrained settings, allowing us to better characterize the role of gravity in perceptual and motor systems.

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

EXPERIMENTAL APPROACHES

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

Hypergravity environments can be created on Earth by means of human centrifuges (DiZio and Lackner 2002). Gravity can be increased by accelerating a gondola attached to a rotating gondola, which induces a centripetal acceleration (a photo of a gondola is available in Fig. 1 of White et al. 2018). From the participants' standpoint, the vectorial sum between gravitational and centripetal accelerations is equivalent to an increase in gravity. There are however two limitations to this approach. The first is the presence of a gravitational gradient inside the gondola induced by the proportional relationship between the rotation radius and the centripetal acceleration (see for instance White et al. 2019). Because the radius is relatively short (typically 2–9 m), and because the gondola is tilted to keep the local gravitational vector aligned with body axis, there is a variation of the sensed gravity between the head and the feet. The second limitation is the presence of Coriolis forces that affect movements orthogonal to the rotation axis and may also affect the sensory apparatus. Such settings are therefore not ideal to focus on gravity per se, but clearly allow studying adaptation to noninertial environments in general and likely engage the same adaptation mechanisms as a change in gravity. Several data sets reviewed below were collected in such centrifuges.

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

Hypogravity environments for human experiments correspond to partial or free falling (gravity <1 *g*), which cannot be generated on Earth for experimentations on humans. Two testing environments have been used: parabolic flights and the orbiting International Space Station (ISS). Parabolic flights offer sequences of 20 s of weightlessness, or up to 32 s for Mars (0.38 *g*) and 25 s for lunar (25 s at 0.16 *g*) environments (Pletser et al. 2012), which are repeated several times per flight (e.g., 30 parabolas are usually performed during each flight). Parabolic flights allow performing experiments with more participants than the number of astronauts in the ISS that can be involved in a study. However, they only allow addressing short-term adaptation due to limited total time of exposure and have similar constraints as those listed for hypergravity exposure. The ISS, in contrast, offers a stable environment but only hosts experiments with a very limited number of astronauts who may not be representative of the general population as they undergo a highly demanding cognitive and motor training program. Hence, understanding the role of gravity in motor control in general requires considering data from distinct environments and contexts. The complexity of these settings and their associated potential confounding factors sometimes challenge the interpretation of the results. However, as we will show, there are consistent observations that emerge across tasks and contexts that together provide insight into the neural basis of gravity-dependent aspects of perceptual and motor tasks.

PERCEPTION OF OUR ENVIRONMENT AND OUR BODY

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

Perception of Vertical Axis

Gravity strongly influences the subjective perception of verticality. Humans show an aesthetic preference for subjective vertical (Gallagher and Ferrè 2018). Perception of vertical is also naturally driven toward the body longitudinal axis (De Vrijer et al. 2008) in the absence of gravitational information, which was conceptualized by the idiotropic vector model (Mittelstaedt 1983). In a subjective orientation task performed during parabolic flights, Lackner and DiZio (2009) found that the perceived vertical in the aircraft was maintained and even slightly improved under hypergravity, whereas it was aligned with the body orientation under zero gravity. This result, illustrated in Fig. 1*A*, is surprising because participants' bodies were physically rotated, and thus the change in body orientation under 0 *g* could be calculated by integrating acceleration signals encoded in the vestibular system and realigning their pointing direction with the vertical of the aircraft. The observation made by Lackner and Dizio that participants were unable to estimate the vertical axis of the aircraft in 0 *g*, in spite of acceleration levels much larger than perceptual thresholds, suggested that instead of integrating rotational vestibular signals, they strongly relied on static somatosensory feedback. Similarly, during microgravity episodes of parabolic flights or during a 9-day spaceflight, participants reported their subjective vertical as mostly defined with respect to their longitudinal body axis (Glasauer and Mittelstaedt 1992). Although subjected to large interindividual differences, these observations were further supported by data collected during Lunar and Martian gravity contexts (de Winkel et al. 2012). In this study, irrespective of the static visual background orientation, participants tended again to align the subjective vertical with the longitudinal body axis for low values of gravity. This is in

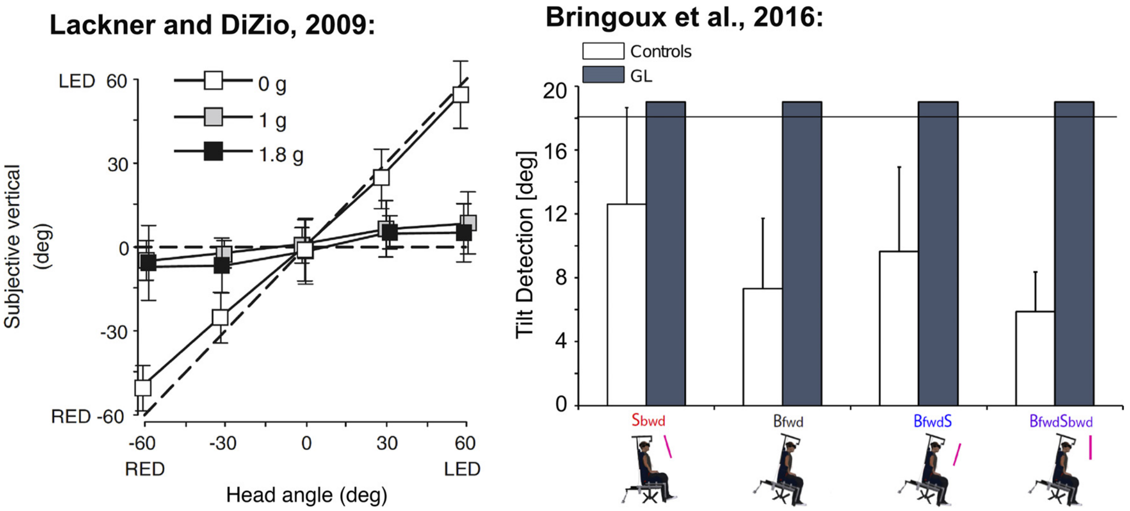


Fig. 1. Perception of external and body orientation. *A*: subjective vertical as a function of head orientation for supine subjects in 3 different gravitational backgrounds. Participants were lying in a rotating bed and were instructed to report the direction of vertical of the aircraft after rotation of the bed. LED, left ear down; RED, right ear down. [Reprinted from Lackner and DiZio (2009).] *B*: mean self-tilt detection thresholds from a vertical orientation as a function of experimental conditions for controls and a deafferented patient (GL) deprived of somatosensory feedback. Conditions are backward rotation of the visual scene (Sbwd), forward rotation of the body without visual scene (Bfwd), forward rotation of the body and visual scene (BfwdS), and forward body rotation without rotation of the scene (BfwdSbfwd). Thresholds for the deafferented patient were arbitrarily set at the minimal value over the manipulated range of tilt (thin line at 18°) as she never felt any tilt sensation up to the largest tilt angle across the different trials in all the conditions she was exposed to. [Reprinted from Bringoux et al. (2016).]

agreement with previous findings from Dyde et al. (2009), during parabolic flights, who reported a decreased influence of static visual tilt on the perception of upright under microgravity conditions. In a subsequent study, Alberts et al. (2016a) developed a Bayesian optimal integration model of this task that demonstrates participants flexibly weigh visual panoramic and vestibular information based on their orientation-dependent reliability.

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

Perception of Body Orientation

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

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

Perception of Object Motion

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

These findings demonstrated a multimodal contribution to the perception of body orientation and of the motion of moving objects in space. Multicue combination has long been proposed to subserve both spatial orientation and object motion perception (Dokka et al. 2015; Mergner et al. 1997; Senot et al. 2005). In addition, recent findings highlighted that varying audiotactile cues about the dynamics of object's fall also impact perceptual estimates such as body height (Tajadura-Jiménez et al. 2018). Importantly, gravity-related cues mediated by somatosensory inputs appear to play a nonnegligible role for self-orientation perception, which is expected to also impact the planning and control of movements [see also Lackner and DiZio (2018) for a recent review on the role of somatosensory inputs for postural control].

SENSORIMOTOR CONTROL

Beyond perception, gravity was found to also play a major role in the control of movements (Lackner and DiZio 2000a; Pozzo et al. 1998). In light of these seminal studies, recent research has explored a broad variety of tasks in different contexts, which together provided insight into the role of gravity in sensorimotor control. Here we present a summary of the findings on goal-directed reaching and object manipulation tasks, highlighting several properties of the neural mechanisms supporting planning and control based on internal representation of the gravitational context.

From Perception to Control

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

An internal representation of gravity within the central nervous system was supported by evidence for transient changes in the velocity profile of pointing movements performed in weightlessness, where directional differences (upward vs. downward) decreased with practice (Gaveau et al. 2016; McIntyre et al. 1998; Papaxanthis et al. 1998b, 2005). The striking observation made across these previous studies was that directional differences in curvature and velocity profiles persisted during the initial phase of exposure to 0 *g*. If direction-dependent effects were simply linked to mechanical interactions between gravity and anatomical constraints, then a change in gravity should have had an instantaneous effect on hand trajectories. Indeed, recent studies highlighted anatomical changes in the brain following exposure to microgravity (Lee et al. 2019; Riascos et al. 2019) or bed rest (Koppelmans et al. 2018). In contrast, the fact that they persisted in 0 *g*, and changed with practice, and the fact that up/down asymmetries occur very early in the movement (Gaveau and Papaxanthis 2011), indicated that they reflected part of the planning of movement (as opposed to a dynamic artifact during execution). This suggests that direction-dependent kinematics emerge from anticipatory processes, or internal priors, based on an internal representation of gravity (Gaveau and Papaxanthis 2011; McIntyre et al. 1998; Papaxanthis et al. 1998a, 1998b, 2005); which likely represents an optimization of the motor plan to include the influence of gravity on the limb (Gaveau et al. 2014, 2016; Wang and Dounskaia 2016).

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

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

With the intent of improving proprioceptive feedback, Bringoux et al. (2012a) investigated whether a gravity-related load applied to the limb helped reduce the constant error of reaching movements performed during microgravity phases of parabolic flights with eyes closed. To that aim, the authors applied a gravity-like torque to the shoulder joint of the moving arm by means of a set of elastic bands attached to the limb. Specifically, the elastic set mimicked the net joint torque exerted at the shoulder in 1 *g* in the range of the different arm angular positions tested, although it is clear that the application of the torque to one point limits the analogy with gravity. As a result, movement kinematics recovered stereotyped patterns as those exhibited on Earth, in spite of the fact that participants (and their vestibular system) were immersed in zero gravity.

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

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

Adaptive Control of Reaching and Pointing

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

More specifically, optimal control approach consists in calculating the best sequence of motor commands with respect to a behavioral performance index and based on knowledge of dynamics (Todorov 2004). The role of gravity in this framework has been considered either by having a component of the performance that explicitly includes mechanical work in the cost function or by maintaining the same cost function, such as a desired final position and velocity, while taking changes in dynamics into account. The two approaches result in an optimal control law that accounts for gravitational forces. In general, predictions obtained in these models have characterized velocity profiles, patterns of muscle activity, and spontaneous movement paths while considering kinematic costs, kinetic costs, and energy expenditures dependent on gravity (Berret et al. 2008, 2011, 2019 for a review; Crevecoeur et al. 2009a; Gaveau et al. 2011, 2014, 2016). An important consideration has been that movement properties changed in a way that was quantitatively captured by the model simulations, which suggests that changes in behavior can be explained in theory. For example, an inactivation principle was introduced to explain kinematic and muscle patterns of varied arm movements performed in the vertical plane (Berret et al. 2008). Specifically, the Minimum Absolute Work model proposes that simultaneous inactivation of both agonist and antagonist muscles demonstrate the minimization of an energy-like criterion (Fig. 2, *A* and *B*).

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

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

The study by Gaveau et al. (2016) highlighted that the difference between the acceleration time and deceleration time of upward and downward movements vanished rapidly during microgravity adaptation. However, this does not mean that movements were symmetric in that respect; in absolute, the symmetry ratio (relative acceleration time with respect to movement time) of a reaching movement may depend on other factors related to the experimental protocol. For instance, Crevecoeur et al. (2010a) also found velocity profiles under microgravity that were similar across up and down movements but whose symmetry ratios (mean $\approx$ 0.45) were slightly smaller than those observed by Gaveau and collaborators in microgravity after adaptation (mean $\approx$ 0.48) or by Gentili and collaborators for horizontal movements (mean in [0.48, 0.5]). Other studies have also reported highly skewed velocity profiles for horizontal movements under normal gravity and during parabolic flights (Crevecoeur et al. 2014), as well as during prolonged exposure to weightlessness in the former orbiting Mir station (Mechtcheriakov et al. 2002). These observations of varying symmetry ratios for horizontal movements may

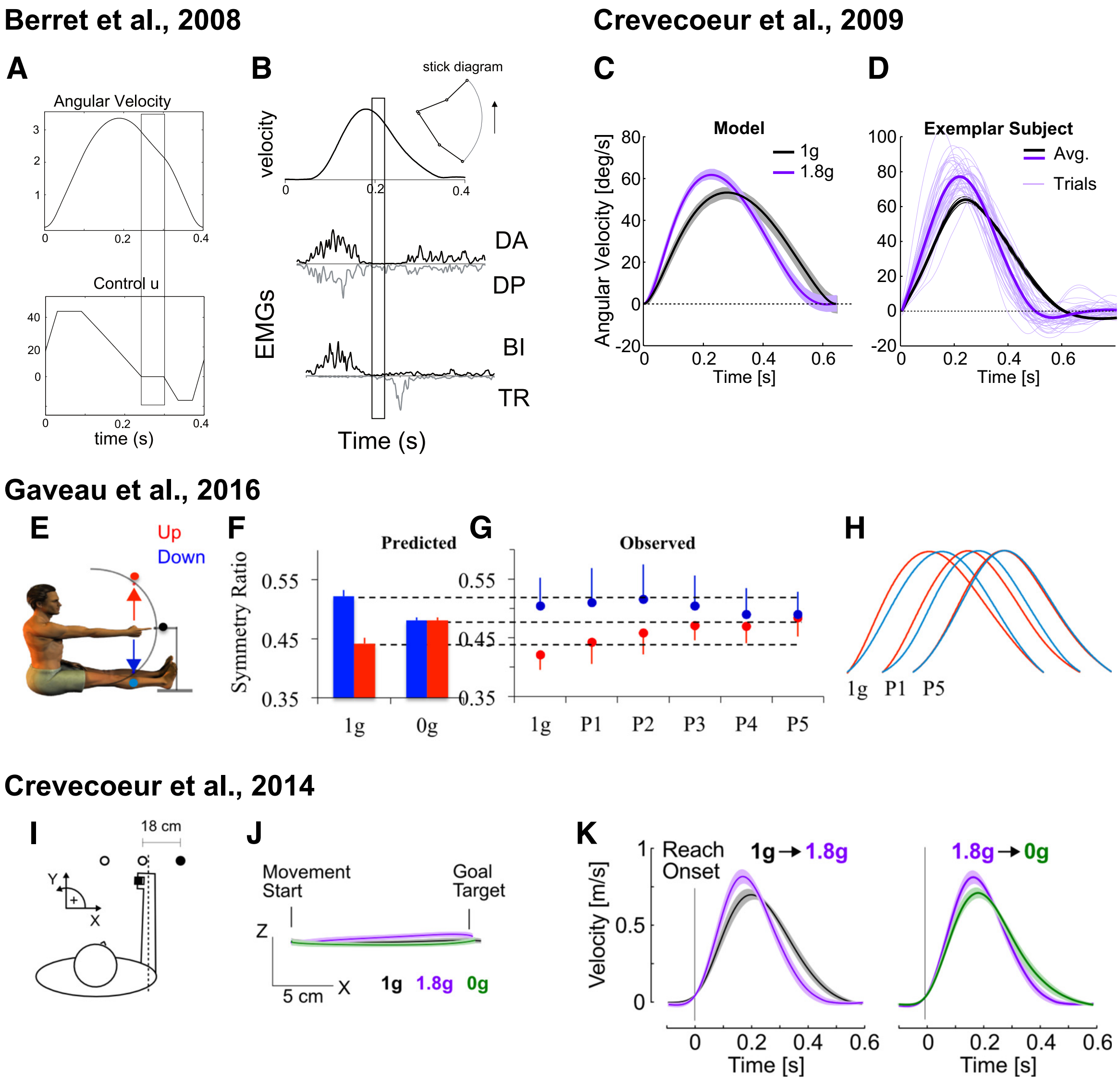


Fig. 2. Adaptation of reaching movements across various gravity levels. *A*: theoretical velocity profiles and control signals derived in the context of optimal control by taking positivity constraints of agonist-antagonist pairs of muscles. The model predicts an interval during which control is equal to 0 (highlighted). *B*: velocity and electromyography (EMG) profiles of deltoid anterior (DA), deltoid posterior (DP), biceps (BI), and triceps (TR) muscles during vertical movements. The interval of inactivation expected in the model is also highlighted. [*A* and *B* adapted from Berret et al. (2008).] *C*: optimal velocity profiles for vertical movements under normal and hypergravity condition. The model was the rotation of a rigid segment with linear actuator. Observe the predicted increase in velocity. *D*: measured velocity profiles under normal and hypergravity from a representative participant. [*C* and *D* adapted from Crevecoeur et al. (2009a).] *E*: participants' initial position and positioning of the 3 targets in the sagittal plane. Eleven participants performed fast and visually guided monoarticular upward and downward arm movements (shoulder rotations in the sagittal plane) under normal gravity (1 *g*) and microgravity conditions (0 *g*) during a parabolic flight (*parabola 1*, P1 to *parabola 5*, P5). *F*: symmetry ratios (acceleration time/movement time) predicted by the minimum smooth-effort model in 1-*g* and in 0-*g* conditions. *G*: symmetry ratios experimentally recorded before (1 *g*) and during adaptation to 0 *g* (P1 to P5). *H*: mean velocity profiles, normalized in amplitude and duration. Qualitative comparisons between upward and downward arm movements illustrate the progressive decrease of directional asymmetries when subjects adapted to the new microgravity environment. [*E–H* adapted from Gaveau et al. (2016).] *I–K*: trajectories and velocity profiles of horizontal movements performed under normal, hyper-, and microgravity. *I*: schematic top view of a participant performing the task. *J*: mean and SE of trajectories in the frontal plane from the point of view of the subject. Traces correspond to rightward movements ($n = 10$ participants). Gravity was aligned with the direction $-Z$. *K*: velocity traces along the *X*-axis across gravitational conditions, highlighting systematic changes following changes in gravity orthogonal to the movement direction. [*I–K* adapted from Crevecoeur et al. (2014).]

relate to instructions about movement accuracy, as they increased with visual feedback, and thus with more stringent control of movement end point (Langolf et al. 1976; Mechtcheriakov et al. 2002; Soechting 1984). These impact of changes in gravity on horizontal movements also indicated that the internal representation of gravity is not simply used to separate gravity-related torque from dynamic ones in the formation of motor commands (Atkeson and Hollerbach 1985; Flanders and Herrmann 1992; Hollerbach and Flash 1982), because changes in gravity also influence horizontal movements where dissociation should leave hand trajectories unaffected.

Another finding across several studies is a general tendency for movement slowing for both vertical and horizontal movements performed in weightlessness (Crevecoeur et al. 2010a, 2014; Mechtcheriakov et al. 2002; White et al. 2008a). The reason why movement slowing occurs is still unclear, although it likely relates to maintaining movement accuracy instead of a sensorimotor deficit (Mechtcheriakov et al. 2002). Theoretical predictions have shown that slowing could mitigate the impact of uncertainty in the internal models of limb dynamics (Crevecoeur et al. 2010a) or optimize the altered dynamics of the task by exploiting system properties such as the resonant frequency when the movement is rhythmic (White et al. 2008a). It was also shown that a mismatch between expected and actual gravity in the internal model of limb dynamics, linked to an error in the estimation of the mass of the limb or of the objects that we manipulate, could at least partially account for movement slowness in microgravity (Crevecoeur et al. 2014). In the latter study, it was hypothesized that a change in weight could be incorrectly attributed to a change in mass, which is a reasonable prior given a life-long experience on Earth. When gravity is not constant, however, this incorrect attribution of an increased weight to the mass generates a mismatch between the true and expected masses, therefore impacting the calibration of motor commands and eventually generating motor errors. In fact, the latter study also provided strong evidence for an integration of gravity in movement planning, as the kinematics of horizontal movements was strongly perturbed by the alternating gravitational phases, revealing a cross-talk between gravity and movement planning even in a direction where the dynamics were unchanged (Fig. 2, *I–K*). Finally, by adopting a different approach, a recent study showed that adiabatic invariants, which determine a property of a system that stays approximately constant when external changes occur slowly, such as gravity, also explain these findings (Boulanger et al. 2019).

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

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

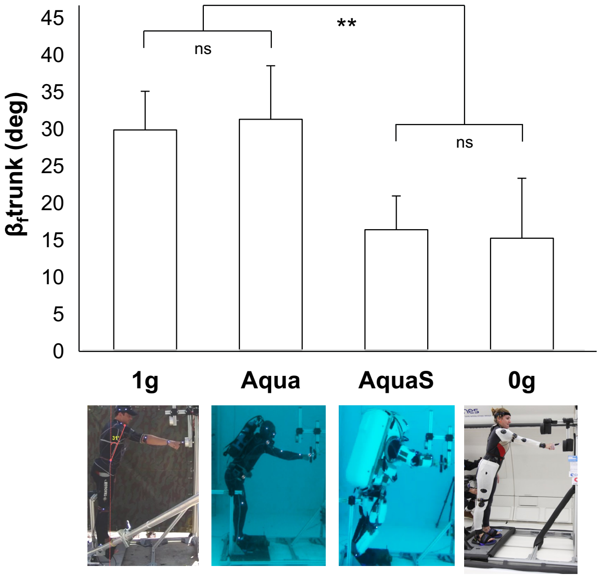


Fig. 3. Different environments implying different force fields on the body are used to investigate whole body goal-directed reaching. From *left* to *right*, conditions represented are normal terrestrial condition (1 *g*), subaquatic condition when immersed in a standard wetsuit (Aqua), subaquatic condition when immersed in a prototypical wetsuit for space training (AquaS), and episodes of microgravity during parabolic flights (0 *g*). Data are the mean final angular position of trunk relative to vertical as a function of the environment for whole body reaching movements toward far targets ($\beta_f$trunk). $^{**}P < 0.01$; ns, nonsignificant difference. [Adapted from Macaluso et al. (2016, 2017).]

Control of Precision Grip during Upper Limb Movements

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

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

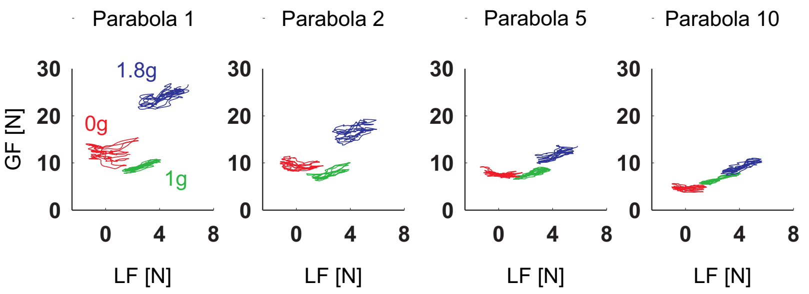
A first study by Hermsdörfer et al. (1999) investigated grip-force adjustments during stationary holding of an object (i.e., without arm movements) and found that the static level of grip force followed both the increase and decrease in object weight induced by parabolic flights. These authors also reported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

In the context of vertical oscillatory movements, the load force oscillates around the object weight, which, under microgravity, generates load force peaks of alternating sign since the weight is zero. At the top of the trajectory, the object tends to keep moving upward. This situation is only experienced in normal gravity for high and unnatural levels of downward acceleration. Previous work reported that, in such tasks, the grip modulation doubled frequency in comparison with normal gravity, likely to counter the inertial peaks occurring both at the top and bottom of cycles (Augurelle et al. 2003; Hermsdörfer et al. 2000). These studies also reported synchronized modulation between grip force and load force, with even a small lead for the grip force, compatible with anticipation (Augurelle et al. 2003).

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

Point-to-point movements performed with a handheld load during parabolic flights revealed a more nuanced story in comparison with oscillatory movements, possibly due to the distinct neural substrates supporting discrete and rhythmic

Augurelle et al., 2003



Opsomer et al., 2018

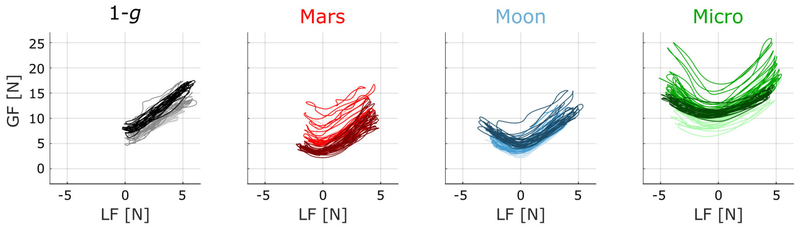


Fig. 4. Grip force adaptation across different gravitational environments. *Top* row: grip force (GF)/load force (LF) modulation is disrupted during the first exposure (*parabola 1*) as highlighted by a large variability and poor linear correlation, except in the 1-*g* condition (green line). Reorganization then occurs over time and normalizes after the 5th parabola. [Adapted from Augurelle et al. (2003).] *Bottom* row: grip force vs. load force traces in a typical subject across conditions of partial gravity corresponding to gravity on the Moon and on Mars. Light, medium and dark traces correspond to early, middle, and late trials, respectively. [Adapted from Opsomer et al. (2018).]

motor tasks (Schaal et al. 2004). In these tasks, inexperienced participants performed movements in weightlessness toward visual targets, separated by short intervals of stationary holding (static phases). The grip force measured during the static phases displayed a slow decrease across parabolas and only stabilized beyond the 10th parabola (Crevecoeur et al. 2009b, 2010b; Giard et al. 2015). In contrast, these studies reported a rather fast adjustment of the grip scaling with changes in load force that paralleled the presence of both positive and negative load force peaks across individual movements, which scaled in amplitude with the inertial loads (Crevecoeur et al. 2010b; Nowak et al. 2001). Indeed, the dynamic modulation of grip force during movement tended to stabilize quicker (<7 parabolas; Crevecoeur et al. 2010b) or even exhibited no evolution across parabolas (Crevecoeur et al. 2009b), which may thus be partially decoupled from the stabilization of the overall grip level, including the static component, which typically takes more than 10 parabolas (>3 min).

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

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

A recent study also showed that practicing a manipulation task under Mars and Moon gravity benefited to the scaling for grip force performed under microgravity (Opsomer et al. 2018) (Fig. 4, *bottom* row). Indeed, the grip-load relationship under zero gravity appeared less disrupted when manipulation was preceded by phases of hypogravity in comparison with the coordination pattern and safety margins reported when naive participants manipulate objects under zero gravity for the first time (Augurelle et al. 2003). In other words, the experience of a previous hypogravity context helped to adjust grip force in a new hypogravity environment, by reducing the safety margin. Yet, the overall safety margin remained higher than under normal gravity, which is indicative of incomplete habituation. This suggests that these rapid behavioral changes are led by direct, or automatic, scaling mechanisms calibrated by the effect of gravity on the body, which interact with other factors linked to volitional control. These observations emphasize again the importance of the information available before the action takes place.

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

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

NEURAL PROCESSING OF GRAVITY

Primary sensory areas have evolved to process information from physical variables encoded in dedicated sensory organs. For instance, information about light encoded in retinal cells converge to primary visual cortex. Likewise, primary somatosensory cortex is the major hub to collect somatosensory feedback. In contrast, there is no dedicated sensory organ for gravity, making perception of the gravity field multisensory in essence. It is therefore expected that the representation of the gravity field emerges through a distributed processing in associative regions or networks.

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

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

While several investigations addressed the question of the internal representation of gravity through visual information (Indovina et al. 2005; Lacquaniti and Maioli 1989; Maffei et al. 2016; McIntyre et al. 2001; Zago et al. 2004; Zago and Lacquaniti 2005c), its neural bases in the absence of vision remain elusive. However, in light of the behavioral evidence reviewed above, it is reasonable to expect the existence of a representation of gravity dependent on somatosensory feedback, likely through an internal model of external forces acting on the limb. Consistent with this idea, White and collaborators found in fMRI studies a selective insular activity during a wrist flexion task when aligned with the vertical, with no visual guidance. Insular activity only emerged in vertical but not horizontal wrist movements (Rousseau et al. 2016a). Furthermore, whether the action was real or mentally simulated also influenced the sub-area of the insula that was active. Actual movements highlighted the posterior insula. In contrast, mentally simulating the movement engaged a more anterior part of the insula (Rousseau et al. 2019). Another recent elegant study, however, suggests that motor imagery of object motion does not rely on an internal model of gravity, but instead resorts to a simulation of visual motion, probably involving mostly visual areas (Gravano et al. 2017). Therefore, it is possible that different parts of the insula may process gravity-relevant feedback in simulated or produced actions that involve the body, while external simulation of the environment may exploit other pathways.

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

Mirroring the complex effects of changes in gravity on behavior, experimental evidence about the neural processing of gravity-related signals for perception and control points to a broad and distributed network including cerebellum, sensorimotor, vestibular, and insular cortices. Indeed, in a rod orientation task, recent results have revealed the importance of dynamic visual cues over static ones in eliciting visual disturbance of verticality in cerebellar patients (Dakin et al. 2018). These results echo similar observations on the ineffectiveness of static visual cues versus the effectiveness of dynamic visual cues in evoking postural responses in cerebellar patients (Bunn et al. 2015; Tarnutzer et al. 2008). Other recent results further confirm that cerebellar function is critical for perception of spatial orientation (MacNeilage and Glasauer 2018). The next steps to deepen our understanding of the neural bases of adaptation to changes in gravity will require addressing important methodological issues such as techniques to measure (deep) brain activities directly in the new gravitational environment.

CONCLUSIONS AND PERSPECTIVES

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

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

How can the rapid but partial adaptation be interpreted? From a conceptual perspective, these results can be captured by considering a parametric representation of gravity in the brain, which impacts perception and control. With such a parametric representation depicted in Fig. 5, the partial adaptation can result from inference about gravity, which, in a probabilistic setting, can vary to some extent due to sensory cues, but not entirely due to strong priors about the invariant nature of gravity on Earth. Here we mean a Bayesian prior about gravity, referring to a value used as default, independent of sensory cues. Following changes in gravity, a posterior estimate of this parameter is formed based on a combination of the prior and the sensory signals. If the prior is narrow about the value of Earth gravity (i.e., our estimate ~1 *g* is accurate), consequence of a life-long experience, the posterior estimate will exhibit a bias toward 1 *g*. As a result, a partial motor adaptation is expected. It should be noted that this conceptual model potentially involves daunting calculations. The reason is that each sensory modality may provide information about gravity in its own encoding scheme and affected by different delays. It was recently suggested that multisensory integration during movement considers different delays (Crevecoeur et al. 2016), but this aspect is still debated (Cluff et al. 2015; Oostwoud Wijdenes and Medendorp 2017), and the processing of a massive change as induced by altered gravity can be a very challenging task.

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

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

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

O.W., J.G., L.B., and F.C. conceived and designed research; O.W., J.G., L.B., and F.C. interpreted results of experiments; O.W., J.G., L.B., and F.C. prepared figures; O.W., J.G., L.B., and F.C. drafted manuscript; O.W., J.G.,

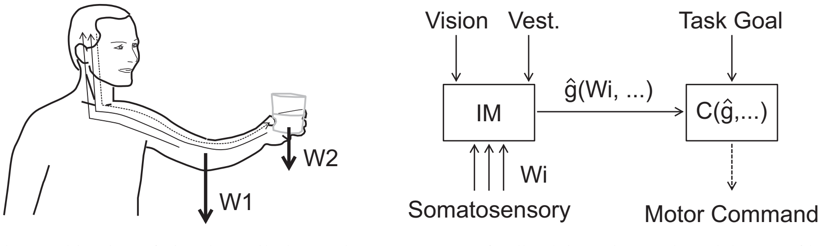

Fig. 5. Schematic illustration of the combination of visual, vestibular, and somatosensory feedback in an internal model (IM) of body and environmental dynamics used to estimate gravity ($\hat{g}$). Somatosensory feedback conveys information about the weight of body segments and held objects (*W1* and *W2*) through muscle and skin afferent feedback (*left*; black arrows). The estimate of gravity is formed by combining the different feedback modalities according to the weights of body parts and of the objects that we manipulate (W_i). This estimate is then used by a motor command generator (C) that depends on $\hat{g}$. Multimodal and gravity-dependent inferences about gravity may explain how motor commands adapt quickly but only partially to the context.

L.B., and F.C. edited and revised manuscript; O.W., J.G., L.B., and F.C. approved final version of manuscript.

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