J Neurophysiol 108: 1685–1694, 2012.
First published June 20, 2012; doi:10.1152/jn.00407.2012.

Does visually induced self-motion affect grip force when holding an object?

Lionel Bringoux,[1] Jean-Claude Lepecq,[1] and Frédéric Danion[2]
[1]*Institute of Movement Sciences, Aix-Marseille University and Centre National de la Recherche Scientifique, Marseille, France; and* [2]*Institute of Neuroscience of la Timone, Aix-Marseille University and Centre National de la Recherche Scientifique, Marseille, France*

Submitted 16 May 2012; accepted in final form 18 June 2012

Bringoux L, Lepecq JC, Danion F. Does visually induced self-motion affect grip force when holding an object? *J Neurophysiol* 108: 1685–1694, 2012. First published June 20, 2012; doi:10.1152/jn.00407.2012.—Accurate control of grip force during object manipulation is necessary to prevent the object from slipping, especially to compensate for the action of gravitational and inertial forces resulting from hand/object motion. The goal of the current study was to assess whether the control of grip force was influenced by visually induced self-motion (i.e., vection), which would normally be accompanied by changes in object load. The main task involved holding a 400-g object between the thumb and the index finger while being seated within a virtual immersive environment that simulated the vertical motion of an elevator across floors. Different visual motions were tested, including oscillatory (0.21 Hz) and constant-speed displacements of the virtual scene. Different arm-loading conditions were also tested: with or without the hand-held object and with or without oscillatory arm motion (0.9 Hz). At the perceptual level, ratings from participants showed that both oscillatory and constant-speed motion of the elevator rapidly induced a long-lasting sensation of self-motion. At the sensorimotor level, vection compellingness altered arm movement control. Spectral analyses revealed that arm motion was entrained by the oscillatory motion of the elevator. However, we found no evidence that grip force used to hold the object was visually affected. Specifically, spectral analyses revealed no component in grip force that would mirror the virtual change in object load associated with the oscillatory motion of the elevator, thereby allowing the grip-to-load force coupling to remain unaffected. Altogether, our findings show that the neural mechanisms underlying vection interfere with arm movement control but do not interfere with the delicate modulation of grip force. More generally, those results provide evidence that the strength of the coupling between the sensorimotor system and the perceptual level can be modulated depending on the effector.

vection; object manipulation; grip force; vision; human

DURING OBJECT manipulation, accurate grip-force control is crucial to prevent slipping at the fingertip. Earlier studies have shown that grip force is tailored to account for changes in object load (Flanagan and Wing 1995; Johansson and Westling 1988; Westling and Johansson 1984). Those changes can be self-induced, for instance when we raise or oscillate our arm, but they can also be externally induced, for instance when we hold an object and our body is submitted to a vertical acceleration (Hermsdörfer et al. 1999). Although the latencies exhibited to adjust grip force depend critically on the nature of the perturbation (self vs. external; see Nowak 2004; Wolpert and Flanagan 2001), a consistent finding is that grip force is scaled in agreement with the current load of the object.

In the context of object manipulation, sensory feedback is crucial to accommodate grip force to the current load of the object. On the one hand, somatosensory feedback (i.e., tactile and proprioceptive feedback) has been demonstrated to be essential to adjust grip force quickly (Danion 2007; Häger-Ross and Johansson 1996; Johansson et al. 1992a; Witney et al. 2004). On the other hand, vision is known to provide critical information before picking up an object (Buckingham and Goodale 2010; Cole 2008; Jenmalm et al. 2000; Lukos et al. 2008) but possibly also once the object has been picked up (Buckingham et al. 2011; Sarlegna et al. 2010). Still, to our knowledge, the possibility that visual information only could trigger grip-force adjustments has never been explicitly tested. In the current experiment, we propose to explore this possibility by means of a visual background displacement producing an optic flow that induces illusory self-motion perception also called vection (for a review, see Riecke 2011).

The rationale underlying our experiment is that if vection gives rise to an (illusory) change in object load, grip force should be altered. As an everyday example, this situation corresponds to the case of a passenger seated in a stationary train, holding a cup of coffee, who is seeing another train leaving the station. The question we want to address here is whether grip force is modulated by the illusory change in load associated with visually induced self-motion perception in Earth-stationary participants. Practically, to answer this question, we tested a set of 10 participants in an immersive virtual reality display, namely a cave automatic virtual environment (CAVE; Cruz-Neira et al. 1993). In this environment, a glass-walled elevator moving vertically between several floors was simulated. Using their right dominant hand, participants had to hold an object while coding the intensity of the self-motion perception with the other hand. Different kinematics of the elevator (i.e., visual motions) were tested so as to manipulate the magnitude of (virtual) changes in object load and/or intensity of vection.

Two alternative hypotheses were envisaged with respect to the effect of vection. On the one hand, we reasoned that grip force could be affected by vection for the following reasons. Indeed, detrimental effects of optic flow have been already shown for other motor behaviors such as postural control (Guerraz and Bronstein 2008; Lestienne et al. 1977; Thurrell and Bronstein 2002; Wei et al. 2010) and arm movement control (Cohn et al. 2000; Dvorkin et al. 2009), whereas similarities between postural control and grip-force control have been reported (Wing et al. 1997). Moreover, a recent experiment performed by our group has shown that despite access to (conflicting) cutaneous/proprioceptive information, delayed visual feedback provided by means of a computer

---

Address for reprint requests and other correspondence: F. Danion, Institut des Neurosciences de la Timone, UMR 7289, Campus santé Timone, 27, boulevard Jean Moulin, 13385 Marseille cedex 5, France (e-mail: frederic.danion@univ-amu.fr).

screen was sufficient to alter the timing of feedforward grip-force modulations, possibly because subjects experienced illusory changes in object load (Sarlegna et al. 2010). Following this scheme, it is plausible that, using immersive environment, downward accelerations of the visual scene should yield an illusion of upward motion of the elevator, leading to illusory increase in object load thereby associated with an increase in grip force.

On the other hand, it is also plausible that grip force is not altered despite vivid sensation of illusory self-motion. Indeed, previous reports have shown that in certain contexts, motor behavior can operate independently of the perceptual/cognitive level (Flanagan and Beltzner 2000; Goodale et al. 1991, 1994). In particular, Flanagan and Beltzner (2000) have convincingly shown that despite the fact that the smaller of two equally weighted objects is consistently judged to be heavier when being lifted (i.e., the so-called "size-weight illusion"), participants learn to scale their fingertip forces adequately.

MATERIALS AND METHODS

Participants. Ten self-proclaimed right-handed participants (4 males and 6 females) participated in this study (age = 27 ± 11 yr). All participants were healthy and gave informed written consent before the study, according to Aix-Marseille University regulations and the 1964 Declaration of Helsinki. The experiment was approved by a local ethics committee.

Apparatus. We used the immersive virtual-reality display (CAVE) housed in the Mediterranean Virtual Reality Center (Fig. 1*A*). It is constituted of a 3-m deep, 3-m wide, and 4-m high cubic space with three vertical screens for walls and a horizontal screen for the floor. The three vertical surfaces were back-projected, and the ground received direct projection with a 1,400- × 1,050-pixel resolution and a 100-Hz frame rate (more details about this setup can be found in Bringoux et al. 2009). A homemade software (ICE) was used to build and control virtual scenarios. The three-dimensional-projected virtual scene consisted of a transparent elevator cabin of 3 m high, 3 m large and 3 m deep, providing a view of a building interior with stairs and floors (Fig. 1*A*). The cabin was made of glass windowpanes structured by horizontal and vertical steel split lines and framed by sustaining poles. Outside the elevator, the building interior (i.e., the moving part of the visual scene) included a never-ending staircase hanging on each wall panel surrounding the cabin (Fig. 1*B*). The rationale for choosing such a visual scene was to increase the degree of realism and ecological relevance because these factors are known to facilitate vection (Riecke et al. 2006).

Participants were seated with their head unconstrained in the immersive environment 1.5 m away from the front wall (corresponding to the center of the elevator cabin; Fig. 1*C*). Their field of vision was entirely stimulated by the visual display (the apparent size of the virtually projected front frame reached 90° in the vertical dimension). A head-tracking system (ARTTRACK) was used to record the participant's head position and orientation at 100 Hz and to update in real-time the stereoscopic images in relation to the participant's point of view.

In some of the experimental conditions, participants had to hold an object between the thumb and the index finger of their right hand (Fig. 1*D*). The hand-held object included two force sensors (ELPM-T1M-25N; Entran Devices, Fairfield, NJ). One force sensor measured the grip force (the force applied perpendicularly to the sensor surface) resulting from the combined action of the thumb and index finger (Danion and Sarlegna 2007; Sarlegna et al. 2010). The other force sensor was used to measure the load force exerted vertically on the object. This load force resulted from the combined action of gravity and the (possible) vertical movement initiated by the participant. Grip surfaces (2 cm in diameter) were covered with sandpaper. The total mass of the equipped object was 0.4 kg. Both load-force and grip-force signals were collected at 1,000 Hz. By using additional markers, kinematics of head, (right) wrist, and object motion were also collected by the ARTTRACK system at 100 Hz.

Procedure. In all trials, participants had to fixate a visual dot projected at eye level on the front windowpane of the elevator cabin. Both fixation on a stationary foreground object and relative motion of mobile background with respect to a stationary foreground are known to facilitate vection (Ohmi et al. 1987; Riecke 2011; Seno et al. 2009). When fixating this point, participants could not see their hand and/or the object.

A first experimental factor (VISUAL) manipulated in this experiment was the visual flow. Depending on the experimental conditions, the

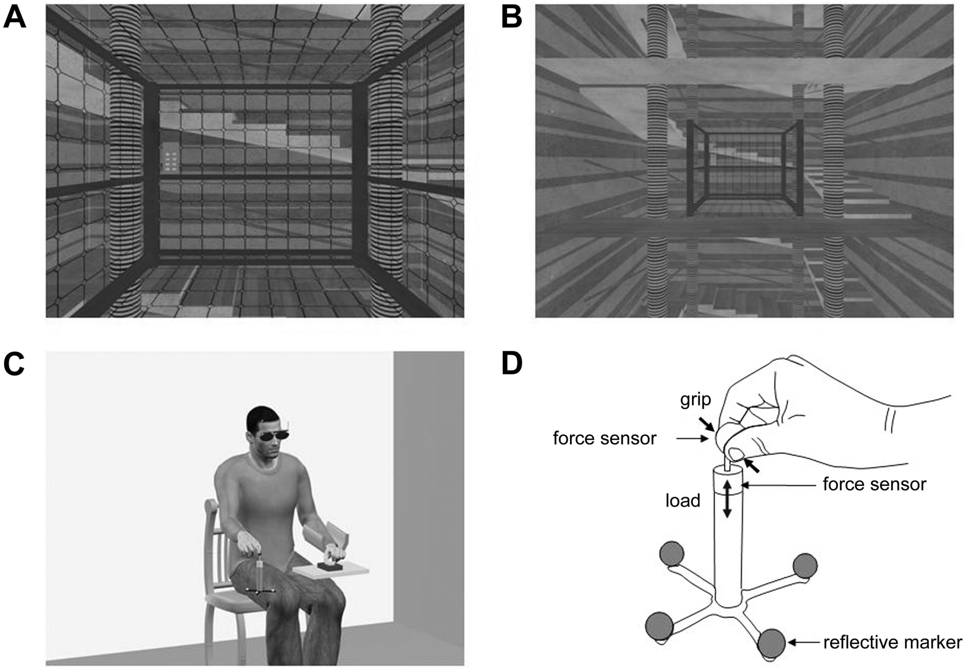

Fig. 1. Experimental setup. *A*: inside view from the virtual elevator cabin. *B*: outside view from the virtual elevator cabin. *C*: illustration of a participant seating in the cave automatic virtual environment (CAVE) and holding the instrumented object while facing the screen. *D*: schematic drawing of the object instrumented with force sensors and reflective markers.

virtual elevator could move at constant speed (VCONST; $v = 1.77$ m/s), stay immobile (STEADY; $v = 0$ m/s), or oscillate. When the elevator oscillated, its frequency was set at 0.21 Hz (period = 4.8 s), a frequency within the range of earlier studies evidencing vertical vection (Wright et al. 2005, 2006, 2009). However, the motion of the elevator was not exactly sinusoidal. This point is made explicit in Fig. 2 that presents the detailed kinematics of the elevator. Indeed, as opposed to a pure sinusoidal motion, the elevator was travelling at either constant speed (50% of the time, in the central portion) or constant acceleration (50% of the time, around the reversal points). The rationale underlying this pattern was to increase the rate of (virtual) load force, which is known to encourage grip-force adjustments (Johansson et al. 1992b). In the example presented in Fig. 2, portions at constant speed were set to ±1.77 m/s and portions at constant acceleration to ± 3 m/s^2 or ±0.3 G. In reference to acceleration, this experimental condition was labeled OSCIL03G. This pattern resulted in an oscillatory movement for which amplitude was ±1.59 m and mean absolute speed was 1.32 m/s. In a second oscillatory experimental condition, labeled OSCIL06G, portions at constant speed were set to ±3.53 m/s, and portions at constant acceleration to ± 6 m/s^2 or ±0.6 G. This resulted in a movement amplitude of ±3.18 m and an average absolute speed of 2.65 m/s. Within a real elevator, OSCIL03G and OSCIL06G would be respectively associated with a fluctuation in object load of ±30 and ±60%. This means that load force would oscillate between 2.8 and 5.2 N in OSCIL03G (Fig. 2, *bottom*) and between 1.6 and 6.4 N in OSCIL06G.

When holding objects, such variations in load are typically accompanied by changes in grip force no matter whether they follow arm movements or whole body motion (Flanagan and Tresilian 1994; Hermsdörfer et al. 1999; Johansson et al. 1992c; Nowak et al. 2002; Westling and Johansson 1984). Specifically, Hermsdörfer et al. (1999) showed that when subjects experience changes in vertical acceleration (0, 1, or 2 G by means of parabolic flights), their grip force was dictated by the ongoing load of the object (see their Figs. 1 and 3). To provide further evidence that grip force is influenced by passive vertical whole body motion, we present in our Fig. 3 some data that we collected on a blindfolded subject who was submitted to even more subtle upward accelerations (with peaks ranging from 0.17 to 0.53 G). Vertical accelerations were obtained by means of a motorized chair that could be servo-controlled (for more details, see Lepecq et al. 1999). The key point is that for each intensity, even the smallest one (0.17 G), grip-force adjustments were elicited (for more details, see Fig. 3 caption).

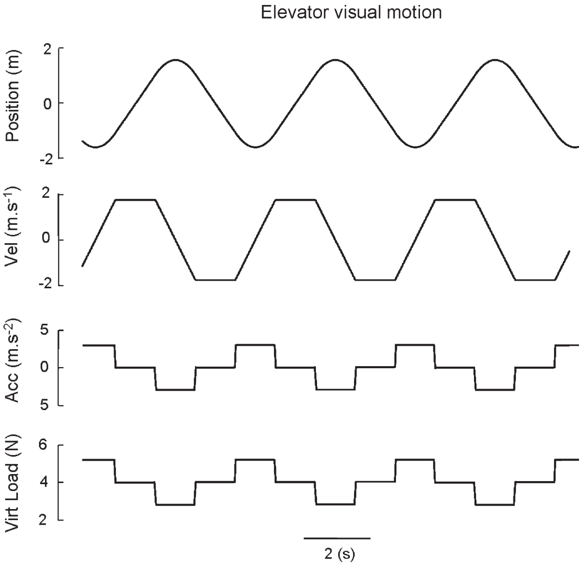

Fig. 2. Kinematics of the virtual (Virt) elevator during oscillatory motion in experimental condition OSCIL03G. The quasisinusoidal pattern yielded successive phases of constant and variable velocity (Vel) based on distinct accelerations (Acc) steps. The *bottom* graph presents the gravitoinertial load of the object that would result from the elevator motion.

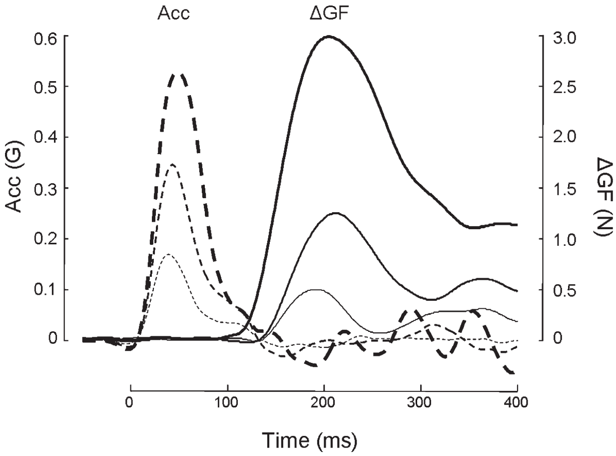

Fig. 3. Grip-force adjustments (ΔGF) elicited by passive upward whole body motion. Each grip-force and acceleration trace represents the mean of 6 individual trials. Dashed and solid lines correspond to acceleration and grip-force signals, respectively. Note that background grip force (i.e., before movement onset) was subtracted.

Overall, the experimental factor VISUAL consisted of four different modalities (OSCIL03G, OSCIL06G, VCONST, and STEADY). In OSCIL03G, OSCIL06G, and VCONST, each trial consisted of 88 s of visual exposure to the moving scene. Data acquisition was initiated 1 s before visual motion began and ended 5 s after visual motion stopped. In the STEADY condition, the same timing was used except that there was no visual motion.

Independently of the visual scene, two other experimental factors were investigated. Depending on the trial, participants could be asked to hold or not the instrumented object with their right hand (OBJECT factor) while oscillating or keeping immobile their right limb (MOVE factor). When an oscillatory movement of the limb was required, the movement frequency was set at 0.9 Hz by means of an auditory metronome (2 beeps per cycle). Concerning movement amplitude, participants were instructed to perform vertical movements of ~20 cm so that upper hand position never exceeds shoulder vertical position. Visual observation of the participants revealed that this vertical motion was essentially produced through the elbow joint. When the instruction was to maintain the arm immobile, hand position corresponded approximately to the center of oscillation in the mobile hand condition. When the task did not require holding the instrumented object, participants wore a 400-g band at the (right) wrist so that the inertia of the arm as well as the gravitational torque exerted on the arm were comparable when holding or not the object. Changes in object load associated with the movement of the arm theoretically corresponded to a modulation of ±30% of the static load, a value that is comparable with the change in virtual load associated with the motion of the elevator. More generally, rhythmic movements were included in our protocol so as to encourage grip-force modulations. We reasoned that grip-force modulations described elsewhere during rhythmical movements (Danion et al. 2009; Flanagan and Wing 1995) could possibly facilitate the emergence of other grip-force modulations (i.e., associated with the virtual load inherent to oscillatory motion of the elevator). Nevertheless, to tease apart grip-force modulations induced by arm movements and those (possibly) induced by optic flow, the frequency of the elevator motion and arm movement were nonharmonic (0.21 vs. 0.9 Hz). Note that when holding the object, participants were not given instructions regarding suitable grip forces (Descoins et al. 2006).

In parallel, except for the STEADY condition, participants were asked to rate the intensity of vection with their left hand by means of a 3-position button with the following conventions: 0, no vection; 1, partial vection; and 2, full vection. As a result, a switch from position 0 to 1 defines vection onset, and a switch from position 1 to 2 corresponds to a transition toward maximal vection intensity. Note that reverse switches (i.e., 2 to 1, 1 to 0) were allowed at any time during the trial. Noticeably, this perceptual task was presented simultaneously with the motor requirements described above to achieve the main goal of the study, that is, investigating the temporal relationship between vection and grip-force control. Participants were familiarized with the different perceptual states and transitions during preliminary warmup trials.

Overall, each of the 3 main VISUAL modalities (OSCIL03G, OSCIL06G, and VCONST) was tested for each the OBJECT and MOVE modality. Given that each combination was tested twice, this led to 24 experimental trials per participant. The order of the experimental conditions was randomized both within and across participants.

At the end of the experiment, each participant performed an extra set of four control trials. The first two trials investigated the behavior of the participants when holding or moving the object while watching the static visual scene (STEADY). These trials assessed the baseline for grip-force control in the absence of visual motion. Finally, in the last two trials, we wished to explore the effect of visual motion in a different way. This time, participants were explicitly instructed to modulate their grip force at the frequency of the visual scene (0.21 Hz). However, participants received no explicit instruction with regard to the way their grip force should be synchronized with the oscillatory movement of the elevator. We reasoned that if the visually perceived movement was associated with a perceived load, a preferred mode of coordination should emerge such that grip force is maximal when the elevator reaches its lowest position (anti-phase coordination) rather than when the elevator reaches its top position (in-phase coordination). No vection coding was required during both these trials and the STEADY ones. Altogether, each participant performed a total of 28 trials, which took on average ~60 min.

Data analysis. Typical recordings in OSCIL03G are illustrated in Fig. 4 for a participant oscillating the instrumented object. All kinematic and kinetic signals were low-pass filtered at 20 Hz (4th-order, no-lag, dual-pass Butterworth). The following dependent variables were extracted from each trial (the instants preceding and following the virtual motion of the elevator were discarded from this particular analysis). Concerning the kinematic of the arm, we analyzed the mean vertical hand/object position and the amplitude of hand/object movement along the vertical axis when an oscillatory movement was required. Concerning kinetic signals, when participants held the object and had to oscillate it, the strength of the coupling between grip force and load force was evaluated by means of cross-correlation; this analysis was performed on a cycle-to-cycle basis (see Danion et al. 2009). We reasoned that if grip force is also regulated as a function of the virtual load associated with the oscillating motion of the elevator, cross-correlation is likely to decrease. To assess further the presence of more subtle effects of vection, fast Fourier transform (FFT) method was applied to grip-force signals over each (entire) trial. We paid particular attention to the amplitude of the FFT component at 0.21 Hz (i.e., frequency of the elevator oscillation). Again, we reasoned that this component was likely to increase if vection influenced grip-force control during oscillatory motion of the elevator. For the sake of comparison, and because previous studies have shown that arm movement could be influenced by a moving scene (Cohn et al. 2000; Dvorkin et al. 2009), similar FFT analysis was conducted on arm vertical motion to assess possible entraining effects of vection in our task. Concerning the control trials in which the participants were explicitly instructed to modulate their grip force at the frequency of the elevator, FFT analyses were also conducted to compute the phase difference between grip force and the elevator motion. Those analyses were conducted on the last 50 s of each trial.

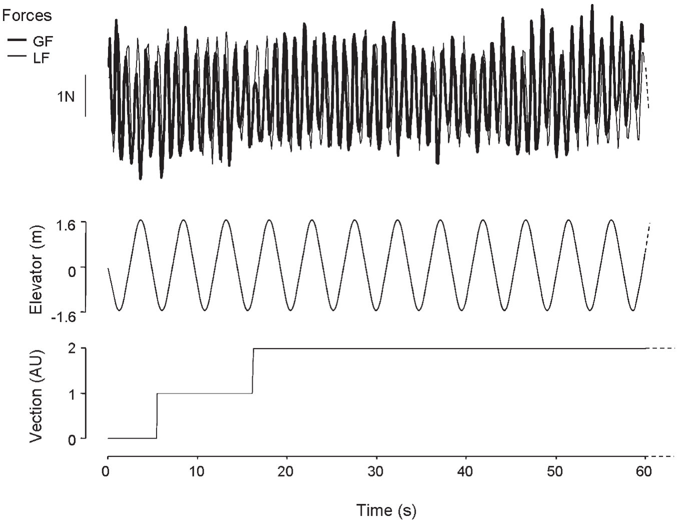

Fig. 4. Typical trial recordings of grip force, load force (LF), elevator position, and vection intensity (in arbitrary units) in the OSCIL03G condition while the participant oscillated the instrumented object. Only the 1st 60 s are presented.

Concerning the perceptual level, the following three dependent variables were extracted over each trial: mean vection intensity (MVI), vection onset (VT1), and full vection onset (VT2).

The main statistical analyses used in this study were ANOVA with OBJECT (with vs. without), MOVE (static vs. mobile), and VISUAL (VCONST, OSCIL03G, and OSCIL06G) as within-subject factors. Newman-Keuls technique was used for post hoc analyses. Since correlation coefficients do not follow a normal distribution, *z*-scores (Fisher transformation) were used for statistical analysis. A 0.05 significance threshold was used for all analyses.

RESULTS

We first report data serving as prerequisites allowing for subsequent analysis of grip-force control. Among these prerequisites are not only the compliance with basic task requirements (e.g., spatiotemporal constraints on arm motion), but also the presence of vection when facing the moving visual scene.

Compliance with basic task requirements. The simultaneous assessment of both perceptual and sensorimotor tasks was not disturbing for the subjects, as none of them reported difficulties in providing online vection ratings while holding an object and/or while moving the arm.

Concerning arm motion, we checked whether task instructions regarding the MOVE factor (i.e., oscillating or keeping immobile the arm) influenced arm kinematics. To that aim, we analyzed vertical displacement of hand/object and assessed whether the amplitude and frequency of movement was within the range of expected values. Over the group, the mean frequency of oscillation was 0.900 ± 0.004 Hz, and the mean amplitude was 22.3 ± 7.0 cm. Concerning the stability of hand/object position in the no-movement condition, we found that the drift in vertical position over each trial was below 1 cm. Similar analysis performed on trials with oscillatory movements showed that the vertical drift in the center of oscillation was below 2 cm. Overall, those analyses suggest that participants complied rather well with our instructions.

Vection ratings. Analysis of perceptual variables confirmed that the visual motion of the elevator was adequate to induce vection. Indeed, pooled across all experimental conditions in which the elevator was mobile (OSCIL03G, OSCIL06G, and

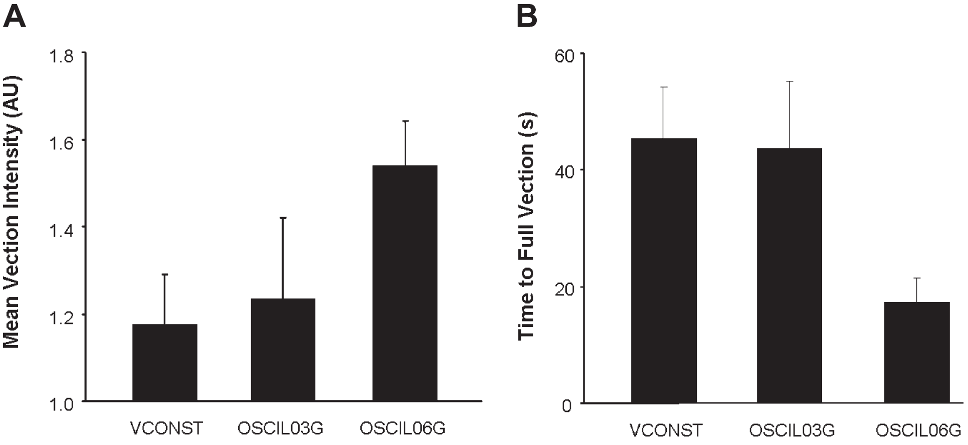

Fig. 5. *A*: mean vection intensity expressed in arbitrary units. *B*: full vection onset time expressed in seconds as a function of experimental conditions. Error bars correspond to SE. VCONST, experimental condition in which virtual elevator could move at constant speed.

VCONST), the MVI was 1.32 ± 0.39 (mean ± SD across subjects). Furthermore, the mean time to enter vection (VT1) and to reach full vection (VT2) were respectively 9.3 ± 7.7 and 35.5 ± 21.3. Altogether, participants spent 85% of trial duration in partial or full vection. Overall, they had no difficulty in perceiving illusory self-motion when the virtual elevator was moved (Fig. 4, *bottom*).

To assess more specifically whether vection was influenced by our experimental factors, each dependent variable (MVI, VT1, and VT2) was submitted to a three-way ANOVA (VISUAL × OBJECT × MOVE). For each of these observations, results showed neither main effect of OBJECT and MOVE nor interaction between any of the three factors ($P > 0.12$), thereby suggesting that holding or not the object, as well as moving or not the hand, did not significantly influence visually induced self-motion. In contrast, the intensity and latency of vection depended on the motion of the elevator. Indeed, we found a significant main effect of VISUAL for both MVI [$F(2,18) = 6.39$, $P < 0.01$; Fig. 5*A*] and VT2 [$F(2,18) = 5.31$, $P < 0.05$; Fig. 5*B*]. In each case, post hoc analyses revealed that values in OSCIL06G differed from those in the other two conditions (OSCIL03G and VCONST, $P < 0.05$). However, there was no significant difference between OSCIL03G and VCONST. Altogether, the condition in which the elevator was oscillating while reaching higher speeds and accelerations (OSCIL06G) was the one that favored the most vection, as reflected by greater vection intensity, and shorter time to reach full vection.

Grip-load force coupling. A key issue in our study was to determine whether grip force could be altered by illusory self-motion. To explore the possible changes in grip force, we investigated first the grip-load force coupling (for conditions in which oscillatory movements of the object were required). Over the group, cross-correlation provided a mean r value of 0.64 ($P < 0.001$) and a mean lag of −50 ms (different from 0, $P < 0.001$). Those values are consistent with the view that changes in grip force and load force were parallel, with grip force preceding slightly load force. However, a one-way ANOVA did not reveal any significant influence of VISUAL on r value [$F(3,27) = 0.59$, $P = 0.62$] and mean lag [$F(3,27) = 0.58$, $P = 0.63$].

Spectral analysis of grip force. Subsequently, the power spectrum of grip force was investigated to look for traces of grip force modulations that would compensate for the virtual load induced by the oscillatory motion of the elevator. Mean group power spectrum of grip force is provided in Fig. 6 when participants were required to oscillate the object while facing our various visual scenes. In line with the instruction of oscillating the object at 0.9 Hz, the power spectrum of grip force exhibits a peak at 0.9 Hz in our four visual conditions. However, no particular increase in grip-force power was found in the vicinity of 0.21 Hz in OSCIL06G and OSCIL03G (the frequency at which the illusory load varied). Apart from the lack of peak at 0.9 Hz, a similar finding was obtained when the object was held static. Furthermore, a one-way ANOVA confirmed that the magnitude of the grip-force component at 0.21 Hz did not change as a function of VISUAL [$F(3,27) = 0.78$, $P = 0.52$]. Altogether, we found no evidence of grip-force modulation that mirrored visually induced self-motion.

Analysis of grip force when the elevator stopped at the end of the trial. To investigate further whether grip force could be influenced by visually induced self-motion, particular attention was paid to the instances at which the elevator stopped while initially travelling at constant speed (VCONST condition). Figure 7 illustrates individual profiles of grip force in the vicinity of the elevator stop ($t = 88$ s). Noticeably, no particular changes in grip force were observed when the elevator

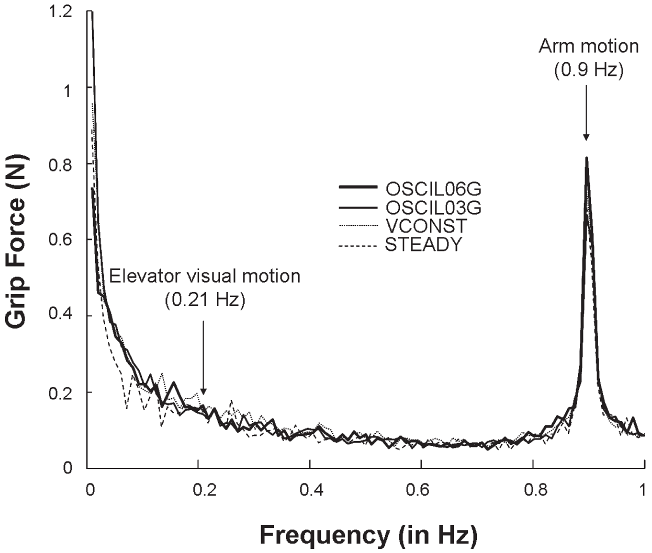

Fig. 6. Mean power spectrum of grip force as a function of the visual scene when the participants had to oscillate the hand-held object. Note the lack of grip-force modulation at the frequency of the oscillating elevator (i.e., OSCIL03G and OSCIL06G). STEADY, experimental condition in which virtual elevator remained immobile.

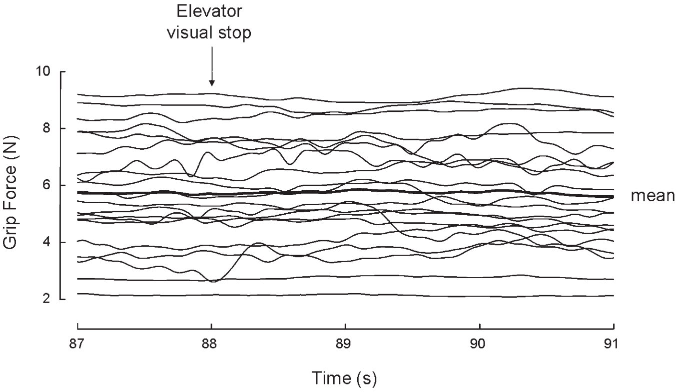

Fig. 7. Grip-force trajectories in the vicinity of the elevator stop in the VCONST condition when holding the object statically. Individual trajectories (20 trials) are represented by thin lines. Mean group trajectory is represented by the thick line. Note the lack of grip-force adjustments despite the abrupt changes in (virtual) load inherent to the elevator stop. This lack of change is poorly influenced by the subject's background grip force.

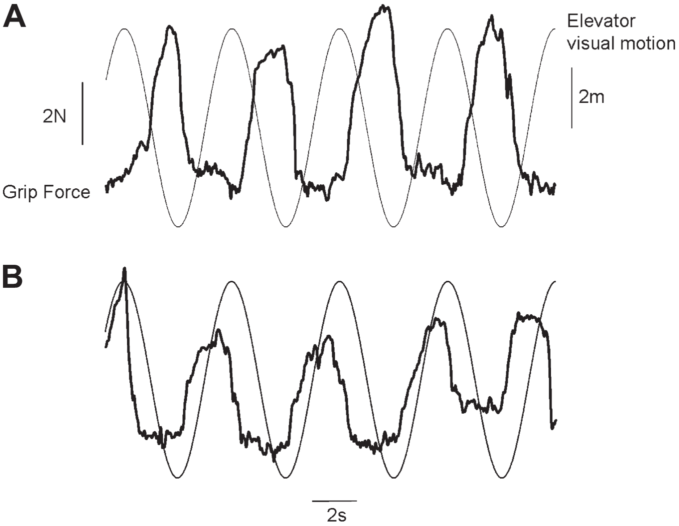

Fig. 8. Examples of coordination between voluntary grip-force modulation and elevator motion during the control trials. The 2 trials were performed by the same subject who adopted successively the anti-phase (*A*) and in-phase (*B*) mode of coordination.

suddenly stopped, despite the fact that the change in virtual load was infinite and that the occurrence of the stop was difficult to predict given the long duration of the trials. Altogether, even when focusing on more abrupt changes in virtual load, we were unable to find evidence that visually induced self-motion could trigger changes in grip force.

Coordination between voluntary grip-force modulation and elevator motion. Control trials in which participants had to squeeze voluntarily the object while being exposed to oscillatory motion of the elevator also supported that visually induced self-motion did not alter grip-force control. Although participants received no explicit instruction with regard to the way their grip force should be synchronized with the motion of the elevator, we found two preferred modes of coordination (Fig. 8). The first mode of coordination corresponded roughly to being in anti-phase with the elevator motion (mean = 136 ± 13°), whereas the second one corresponded to being in-phase (mean = −37 ± 28°). Among the group, three participants adopted consistently an anti-phase coordination, three others kept the in-phase coordination, and the four last ones switched between coordination modes across the two trials (see Fig. 8 for an example). Altogether, we found no evidence that anti-phase coordination with the elevator (leading to grip force being in-phase with the virtual load) was favored compared with in-phase coordination.

Spectral analysis of arm movement. To investigate whether arm movement could be possibly influenced by the oscillatory motion of the elevator, we also performed power spectral analyses of arm vertical position. Mean group power spectrum are provided in Fig. 9 for each visual scene while participants had to oscillate their arm/object. In line with this instruction, the power spectrum of the arm exhibits a peak at 0.9 Hz in all visual conditions. Although substantially smaller, this spectral analysis also revealed the existence of a second peak at 0.21 Hz in conditions in which the elevator was oscillating (OSCIL03G and OSCIL06G).[1] However, no similar peak was observed under conditions VCONST and STEADY (see the Fig. 9 *inset* that zooms on the peak). This view was supported by a one-way ANOVA showing a main effect of VISUAL [$F(3,21) = 13.63$, $P < 0.001$]. Post hoc analyses revealed that power at 0.21 Hz in OSCIL03G and OSCIL06G was significantly greater than in VCONST and STEADY ($P < 0.01$), but there was no significant difference between OSCIL03G and OSCIL06G ($P = 0.17$). Rather, similar findings were observed when the hand/object was held statically; however, the effect of VISUAL barely reached the level of significance ($P = 0.054$). Overall, the spectral analyses showed that arm motion was more influenced by the oscillatory motion of the elevator when the arm was also oscillating. To characterize further the movements induced by OSCIL03G and OSCIL06G at 0.21 Hz (i.e., when participants had to oscillate the arm/object), we computed the phase lag between these induced movements and the motion of the elevator. Figure 10 presenting the polar

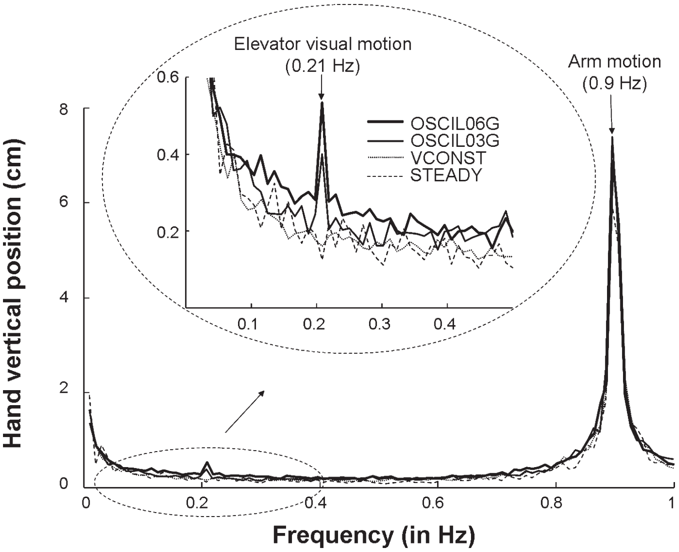

Fig. 9. Mean power spectrum of hand vertical position during oscillatory motion of the hand. Each visual condition is treated separately. Data from conditions with and without a hand-held object are pooled together. Note the increased oscillations of the arm at 0.21 Hz (the frequency of the elevator in OSCIL03G and OSCIL06G). The *inset* provides a zoom on this phenomenon.

---

[1] Given their amplitude and frequency, the visually induced movements only led to tiny changes in object load (<0.002 N) that were unlikely to elicit any grip-force adjustments.

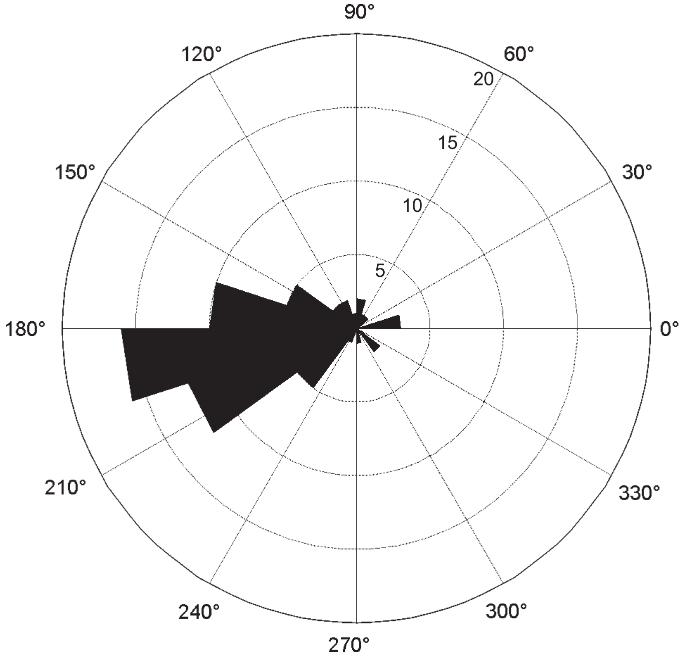

Fig. 10. Polar distribution of the phase lag between the visually induced motion of the hand/object and the motion of the elevator. Data refer to the conditions OSCIL03G and OSCIL06G in which the participants were explicitly instructed to oscillate the hand/object. Data from conditions with and without a hand-held object are pooled together. Note the existence of a preferred mode of coordination between the 2 movements (i.e., anti-phase).

distribution of this phase lag shows that, in most cases, the visually induced movement was in anti-phase with the motion of the elevator.

DISCUSSION

Results of the present study showed that grip-force modulation was not influenced per se by visually induced self-motion. This core finding is mainly supported by the lack of change in grip force during visually induced oscillatory motion (OSCIL03G and OSCIL06G) or abrupt stops of the elevator (VCONST). These data were subsequently reinforced by control tests showing that participants showed no preference to squeeze (voluntarily) the object in phase or in anti-phase with the virtual load resulting from the oscillatory motion of the elevator. As an aside, we also found that holding an object, as well as moving the arm, did not influence vection. Finally, in contrast to grip force, the analysis of arm motion revealed some entraining effects of the visual scene during oscillatory motion of the elevator (OSCIL03G and OSCIL06G). We propose now to discuss more extensively those results and their implications.

Was vection enough compelling to alter sensorimotor processes? The fact that previous studies have shown that vection could influence postural control (Guerraz and Bronstein 2008; Lestienne et al. 1977; Thurrell and Bronstein 2002; Wei et al. 2010), whereas here we found no evidence that grip-force control was influenced by vection, raises the question as to whether our visual stimulus was enough compelling to alter sensorimotor processes. The fact that arm motion was influenced by vection makes this hypothesis unlikely. Briefly, we have found augmented oscillations of the arm in OSCIL03G and OSCIL06G at the frequency of the visual scene (0.21 Hz), especially when the arm was already oscillating voluntarily (0.9 Hz). The key point is that most of those visually induced arm oscillations were in anti-phase with the elevator motion. Note that within a real elevator that oscillates, gravitoinertial forces are maximal at the bottom and minimal at the top. Thus, if participants tried to compensate, at least partly, the (illusory) change in arm load associated with the visual motion of the virtual elevator, it makes sense that their arm was moving up when the elevator was going down (and vice versa). Furthermore, this scheme receives support from another study in which stationary subjects who experienced illusory self-rotation (by means of rotating visual flow) made reaching errors that were consistent with an attempt to compensate for (virtual) Coriolis forces (Cohn et al. 2000).

Concerning the fact that visually induced arm motion was more easily provoked during ongoing cyclical arm movement (as compared with static arm posture), we reason that the large and constantly varying muscle torques required to sustain a cyclical arm movement impaired the ability of the participants to detect the lack of change in gravitoinertial forces. This hypothesis fits well with other observations showing that our ability to perceive muscle effort is attenuated during an ongoing movement (Collins et al. 1998). Overall, the analysis of arm motion in our study suggests that the visual motion of the elevator was compelling enough to alter sensorimotor processes. As a result, we conclude that insufficient vividness of vection is unlikely to account for the lack of grip-force alterations.

Did simultaneous vection ratings prevent alteration in grip-force control? One might also argue that grip force did not suffer from visual illusions because, in the present experiment, participants were fully involved in vection coding and consequently allocated insufficient attentional resources to the motor task (i.e., controlling the hand-held object). However, there are previous reports indicating that two perceptual tasks, or one perceptual task and one motor task, can be achieved simultaneously with no interference (i.e., without eliciting any “collateral impairments”). For instance, Seno et al. (2009) investigated the temporal relationship between the occurrence of two illusions (i.e., vection and figure-ground reversals) by continuously asking for a binary judgment on both percepts. In the same vein, Thilo and Gresty (2002) simultaneously recorded the perception of visually induced self-motion and the estimation of postural verticality. As in the present experiment, the subjects did not report any difficulty to perform both tasks simultaneously.

Reciprocally, if dual-tasking was critical in our study, one could also reason that changing the requirements of the motor task (i.e., modulating task difficulty) should influence the vection ratings. However, in contrast to the moving scene characteristics, our results showed that neither holding an object nor moving the arm yielded a change on vection chronometry and intensity. Overall, the framework of cognitive load and attentional resources (Sweller 1988) would suggest that the attentional demand required to achieve simultaneously our perceptual and motor tasks did not exceed the cognitive resources of the subjects.

How contextual is the visual influence on grip-force control? In our previous study showing that visual information could influence grip-force control (Sarlegna et al. 2010), we proposed that delayed visual feedback biased the internal representation of the object and that participants adjusted their grip force so as to accommodate a virtual load. Then why did the virtual load induced by the visual motion of the virtual elevator not alter grip force as well? We see at least two possible reasons. First, in contrast to the current experiment, participants of the delayed feedback experiment were not informed that visual feedback was biased. It is possible that explicit knowledge about the manipulation of visual information weakened its ability to interfere with grip force. In addition, it is very unlikely that participants expected that the chair on which they were seated could move vertically. The context would be obviously different for a passenger seated in a train, holding a cup of coffee, who is expecting the train to leave (Lepecq et al. 1995; Wright and Glasauer 2006). A second possibility lies in the fact that delayed visual feedback and elevator motion alter differently the resulting load of the object and as a consequence may have been concerned with different aspects of grip-force control. Indeed, in Sarlegna et al. (2010), the magnitude of the virtual load (for a given visual delay) remained a function of arm motion, whereas in the current experiment, the virtual load did not depend on the arm motion but was fully determined by the elevator motion. Altogether, this means that the virtual load was self-induced in the first case, whereas it was externally induced in the latter case. Given that the control of grip force for self- and externally induced loads are fundamentally different (Nowak 2004; Wolpert and Flanagan 2001), those results may be interpreted as evidence that reactive mechanisms are more robust to biased visual information than predictive ones.

Flexible relations between perceptual and sensorimotor processes. On the one hand we showed that arm motion was influenced by visual illusions, but on the other hand we also show that grip force was not affected by visual illusions. In line with our grip-force data, other work performed in the context of visual illusions have advocated for the relative independence between perceptual and sensorimotor processes. For instance, it has been shown that visual illusions affecting the perception of either object location (e.g., induced Roelofs effect) or object size (e.g., size-contrast illusions) do not interfere with grasping skills when considering respectively the unaffected reaching accuracy (Bridgeman et al. 2000) or the still-adapted grip aperture (Aglioti et al. 1995; Daprati and Gentilucci 1997). However, the possibility that hand and arm actions could be affected differently by a visual illusion has been less documented. To date, we are only aware of two studies supporting this possibility, both of them performed in the context of the Ponzo (or railway-lines) illusion (Brenner and Smeets 1996; Jackson and Shaw 2000). Specifically, these studies demonstrated that, although size illusions did not influence hand-grip aperture when reaching and grasping an object, it subsequently influenced the speed at which the arm lifted the object (which in turn also affected grip force). Overall, the present work provides further evidence that the strength of the coupling between perceptual and sensorimotor processes can be substantially modulated depending on the effector. More specifically, the novel contribution of our study is to extend this observation to when two effectors (hand and arm) are simultaneously engaged within the same task even though fine coordination between them is required (Flanagan and Johansson 2009; Kawato 1999).

Although our results show separate effects of vection on hand and arm actions, it remains to clarify why this happened. As a possible line of reasoning, we want to emphasize that, in our task, grip-force and arm-motion control relied differently on cutaneous information. Although it is not obvious how cutaneous information could be helpful to monitor the current load of the arm in our task, its contribution is often evoked when evaluating the load of hand-held objects (Cole and Abbs 1988; Johansson et al. 1992a; Monzée et al. 2003; Witney et al. 2004). Assuming that cutaneous information is more difficult to overrule by vection could account for the differential effects on grip force and arm motion. Obviously, at this stage, this is a speculative hypothesis and will require further testing. Assessing the effect of visual illusions in the context of anesthetized fingers would certainly be helpful. At a more general level, we insisted in the Introduction on the similarity between postural control and grip-force control. However, to date, this similarity was mostly demonstrated in the context of anticipatory adjustments (Wing et al. 1997). Because the current experiment targeted more reactive adjustments than anticipatory ones, a possible implication is that the similarity between grip force and posture may not extend to reactive control.

Concluding comments. The current study demonstrates that arm movement is altered by illusory self-motion but at the same time also shows that grip force is not affected by illusory self-motion. Altogether, and despite ongoing debates (Brogaard 2011; Coello et al. 2007), our grip-force data provide further evidence that, in certain cases, perceptual and sensorimotor processes can operate independently (Flanagan and Beltzner 2000; Goodale et al. 1991, 1994). Although the mechanisms and experimental conditions leading to this dissociation remain to be clarified, the novel contribution of our study is to demonstrate that the link between perception and sensorimotor processes is flexible enough to alter differently proximal and distal effectors despite the fact that they need to be finely coordinated for object manipulation (Flanagan and Johansson 2009; Kawato 1999).

ACKNOWLEDGMENTS

We are grateful to Cedric Goulon for programming skills and computer-assisted graphic design, to Frank Buloup for electronic support, and to Jean-Marie Pergandi for graphical help. We thank Jean Blouin for assisting data collection on the motorized chair. Last, we also thank Fabrice Sarlegna and the anonymous reviewers for their valuable comments and suggestions on previous versions of the manuscript.

GRANTS

This work was supported by a grant from the Institute of Movement Sciences.

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS

L.B., J.-C.L., and F.D. conception and design of research; L.B., J.-C.L., and F.D. performed experiments; L.B., J.-C.L., and F.D. analyzed data; L.B., J.-C.L., and F.D. interpreted results of experiments; L.B., J.-C.L., and F.D. prepared figures; L.B., J.-C.L., and F.D. drafted manuscript; L.B., J.-C.L., and F.D. edited and revised manuscript; L.B., J.-C.L., and F.D. approved final version of manuscript.

REFERENCES

Aglioti S, DeSouza JF, Goodale MA. Size-contrast illusions deceive the eye but not the hand. *Curr Biol* 5: 679–685, 1995.

Brenner E, Smeets JB. Size illusion influences how we lift but not how we grasp an object. *Exp Brain Res* 111: 473–476, 1996.

Bridgeman B, Gemmer A, Forsman T, Huemer V. Processing spatial information in the sensorimotor branch of the visual system. *Vision Res* 40: 3539–3552, 2000.

Bringoux L, Bourdin C, Lepecq JC, Sandor PM, Pergandi JM, Mestre D. Interaction between reference frames during subjective vertical estimates in a tilted immersive virtual environment. *Perception* 38: 1053–1071, 2009.

Brogaard B. Conscious vision for action versus unconscious vision for action? *Cogn Sci* 35: 1076–1104, 2011.

Buckingham G, Goodale MA. Lifting without seeing: the role of vision in perceiving and acting upon the size weight illusion. *PLoS One* 5: e9709, 2010.

Buckingham G, Ranger NS, Goodale MA. The role of vision in detecting and correcting fingertip force errors during object lifting. *J Vis* 11: 4, 2011.

Coello Y, Danckert J, Blangero A, Rossetti Y. Do visual illusions probe the visual brain? Illusions in action without a dorsal visual stream. *Neuropsychologia* 45: 1849–1858, 2007.

Cohn JV, DiZio P, Lackner JR. Reaching during virtual rotation: context specific compensations for expected coriolis forces. *J Neurophysiol* 83: 3230–3240, 2000.

Cole KJ, Abbs JH. Grip force adjustments evoked by load force perturbations of a grasped object. *J Neurophysiol* 60: 1513–1522, 1988.

Cole KJ. Lifting a familiar object: visual size analysis, not memory for object weight, scales lift force. *Exp Brain Res* 188: 551–557, 2008.

Collins DF, Cameron T, Gillard DM, Prochazka A. Muscular sense is attenuated when humans move. *J Physiol* 508: 635–643, 1998.

Cruz-Neira C, Sandin D, DeFanti T. Surround-screen projection-based virtual reality: the design and implementation of the CAVE. In: *Proceedings of the 20th Annual Conference on Computer Graphics and Interactive Techniques*. New York: ACM SIGGRAPH, 1993, p. 135–142.

Danion F, Descoins M, Bootsma RJ. When the fingers need to act faster than the arm: coordination between grip force and load force during oscillation of a hand-held object. *Exp Brain Res* 193: 85–94, 2009.

Danion F, Sarlegna FR. Can the human brain predict the consequences of arm movement corrections when transporting an object? Hints from grip force adjustments. *J Neurosci* 27: 12839–12843, 2007.

Danion F. The contribution of non-digital afferent signals to grip force adjustments evoked by brisk unloading of the arm or the held object. *Clin Neurophysiol* 118: 146–154, 2007.

Daprati E, Gentilucci M. Grasping an illusion. *Neuropsychologia* 35: 1577–1582, 1997.

Descoins M, Danion F, Bootsma RJ. Predictive control of grip force when moving object with an elastic load applied on the arm. *Exp Brain Res* 172: 331–342, 2006.

Dvorkin AY, Kenyon RV, Keshner EA. Effects of roll visual motion on online control of arm movement: reaching within a dynamic virtual environment. *Exp Brain Res* 193: 95–107, 2009.

Flanagan J, Johansson R. Sensorimotor control of manipulation. In: *Encyclopedia of Neuroscience*. Oxford, UK: L. Squire, 2009, p. 593–604.

Flanagan JR, Beltzner MA. Independence of perceptual and sensorimotor predictions in the size-weight illusion. *Nat Neurosci* 3: 737–741, 2000.

Flanagan JR, Tresilian JR. Grip-load force coupling: a general control strategy for transporting objects. *J Exp Psychol Hum Percept Perform* 20: 944–957, 1994.

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

Goodale MA, Meenan JP, Bülthoff HH, Nicolle DA, Murphy KJ, Racicot CI. Separate neural pathways for the visual analysis of object shape in perception and prehension. *Curr Biol* 4: 604–610, 1994.

Goodale MA, Milner AD, Jakobson LS, Carey DP. A neurological dissociation between perceiving objects and grasping them. *Nature* 349: 154–156, 1991.

Guerraz M, Bronstein AM. Mechanisms underlying visually induced body sway. *Neurosci Lett* 443: 12–16, 2008.

Häger-Ross C, Johansson RS. Nondigital afferent input in reactive control of fingertip forces during precision grip. *Exp Brain Res* 110: 131–141, 1996.

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

Jackson SR, Shaw A. The Ponzo illusion affects grip-force but not grip-aperture scaling during prehension movements. *J Exp Psychol Hum Percept Perform* 26: 418–423, 2000.

Jenmalm P, Dahlstedt S, Johansson RS. Visual and tactile information about object-curvature control fingertip forces and grasp kinematics in human dexterous manipulation. *J Neurophysiol* 84: 2984–2997, 2000.

Johansson RS, Häger C, Bäckström L. Somatosensory control of precision grip during unpredictable pulling loads. III. Impairments during digital anesthesia. *Exp Brain Res* 89: 204–213, 1992a.

Johansson RS, Häger C, Riso R. Somatosensory control of precision grip during unpredictable pulling loads. II. Changes in load force rate. *Exp Brain Res* 89: 192–203, 1992b.

Johansson RS, Riso R, Häger C, Bäckström L. Somatosensory control of precision grip during unpredictable pulling loads. I. Changes in load force amplitude. *Exp Brain Res* 89: 181–191, 1992c.

Johansson RS, Westling G. Programmed and triggered actions to rapid load changes during precision grip. *Exp Brain Res* 71: 72–86, 1988.

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

Lepecq JC, Giannopulu I, Baudonniere PM. Cognitive effects on visually induced body motion in children. *Perception* 24: 435–449, 1995.

Lepecq JC, Giannopulu I, Mertz S, Baudonnière PM. Vestibular sensitivity and vection chronometry along the spinal axis in erect man. *Perception* 28: 63–72, 1999.

Lestienne F, Soechting J, Berthoz A. Postural readjustments induced by linear motion of visual scenes. *Exp Brain Res* 28: 363–384, 1977.

Lukos JR, Ansuini C, Santello M. Anticipatory control of grasping: independence of sensorimotor memories for kinematics and kinetics. *J Neurosci* 28: 12765–12774, 2008.

Monzée J, Lamarre Y, Smith AM. The effects of digital anesthesia on force control using a precision grip. *J Neurophysiol* 89: 672–683, 2003.

Nowak DA, Glasauer S, Meyer L, Mait N, Hermsdörfer J. The role of cutaneous feedback for anticipatory grip force adjustments during object movements and externally imposed variation of the direction of gravity. *Somatosens Mot Res* 19: 49–60, 2002.

Nowak DA. Different modes of grip force control: voluntary and externally guided arm movements with a hand-held load. *Clin Neurophysiol* 115: 839–848, 2004.

Ohmi M, Howard IP, Landolt JP. Circular vection as a function of foreground-background relationships. *Perception* 16: 17–22, 1987.

Riecke B. Compelling self-motion through virtual environments without actual self-motion: using self-motion illusions ("vection") to improve user experience in VR. In: *Virtual Reality*, edited by Kim J-J. Rijeka, Croatia: InTech, 2011, chapt. 8, p. 149–176.

Riecke BE, Schulte-Pelkum J, Avraamides MN, Heyde MV, Bülthoff HH. Cognitive factors can influence self-motion perception (vection) in virtual reality. *ACM Trans Appl Percept* 3: 194–216, 2006.

Sarlegna FR, Baud-Bovy G, Danion F. Delayed visual feedback affects both manual tracking and grip force control when transporting a handheld object. *J Neurophysiol* 104: 641–653, 2010.

Seno T, Ito H, Sunaga S. The object and background hypothesis for vection. *Vision Res* 49: 2973–2982, 2009.

Sweller J. Cognitive load during problem solving: effects on learning. *Cogn Sci* 12: 257–285, 1988.

Thilo KV, Gresty MA. Visual motion stimulation, but not visually induced perception of self-motion, biases the perceived direction of verticality. *Brain Res Cogn Brain Res* 14: 258–263, 2002.

Thurrell AE, Bronstein AM. Vection increases the magnitude and accuracy of visually evoked postural responses. *Exp Brain Res* 147: 558–560, 2002.

Wei K, Stevenson IH, Körding KP. The uncertainty associated with visual flow fields and their influence on postural sway: Weber's law suffices to explain the nonlinearity of vection. *J Vis* 10: 4, 2010.

Westling G, Johansson RS. Factors influencing the force control during precision grip. *Exp Brain Res* 53: 277–284, 1984.

Wing AM, Flanagan JR, Richardson J. Anticipatory postural adjustments in stance and grip. *Exp Brain Res* 116: 122–130, 1997.

Witney AG, Wing A, Thonnard JL, Smith AM. The cutaneous contribution to adaptive precision grip. *Trends Neurosci* 27: 637–643, 2004.

Wolpert DM, Flanagan JR. Motor prediction. *Curr Biol* 11: R729–R732, 2001.

Wright WG, DiZio P, Lackner JR. Vertical linear self-motion perception during visual and inertial motion: more than weighted summation of sensory inputs. *J Vestib Res* 15: 185–195, 2005.

Wright WG, DiZio P, Lackner JR. Perceived self-motion in two visual contexts: dissociable mechanisms underlie perception. *J Vestib Res* 16: 23–28, 2006.

Wright WG, Glasauer S. Subjective somatosensory vertical during dynamic tilt is dependent on task, inertial condition, and multisensory concordance. *Exp Brain Res* 172: 310–321, 2006.

Wright WG, Schneider E, Glasauer S. Compensatory manual motor responses while object wielding during combined linear visual and physical roll tilt stimulation. *Exp Brain Res* 192: 683–694, 2009.