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Zago, Myrka, Gianfranco Bosco, Vincenzo Maffei, Marco Iosa, Yuri P. Ivanenko, and Francesco Lacquaniti. Fast adaptation of the internal model of gravity for manual interceptions: evidence for event-dependent learning. J Neurophysiol 93: 1055–1068, 2005. First published September 29, 2004; doi:10.1152/jn.00833.2004. We studied how subjects learn to deal with two conflicting sensory environments as a function of the probability of each environment and the temporal distance between repeated events. Subjects were asked to intercept a visual target moving downward on a screen with randomized laws of motion. We compared five protocols that differed in the probability of constant speed (0g) targets and accelerated (1g) targets. Probability ranged from 9 to 100%, and the time interval between consecutive repetitions of the same target ranged from about 1 to 20 min. We found that subjects systematically timed their responses consistent with the assumption of gravity effects, for both 1g and 0g trials. With training, subjects rapidly adapted to 0g targets by shifting the time of motor activation. Surprisingly, the adaptation rate was independent of both the probability of 0g targets and their temporal distance. Very few 0g trials sporadically interspersed as catch trials during immersive practice with 1g trials were sufficient for learning and consolidation in long-term memory, as verified by retesting after 24 h. We argue that the memory store for adapted states of the internal gravity model is triggered by individual events and can be sustained for prolonged periods of time separating sporadic repetitions. This form of event-related learning could depend on multiple-stage memory, with exponential rise and decay in the initial stages followed by a sample-and-hold module.

INTRODUCTION

Interception of a falling object requires the estimate of time-to-contact (TTC) (Lee et al. 1983). Although the human visual system poorly estimates arbitrary accelerations (Port et al. 1997; Werkhoven et al. 1992), the specific acceleration of gravity (1g) is a terrestrial invariant that is monitored by the vestibular system (Angelaki 2004), and the consequences of its effects on objects are presumably learned and internalized permanently through experience. By combining an internal 1g model with visual information about instantaneous distance and velocity of a target, the nervous system can account for the acceleration of a falling object and more accurately predict TTC (Lacquaniti and Maioli 1989b; Lacquaniti et al. 1993).

We recently introduced a novel paradigm for investigating adaptation of the 1g model to changed environmental conditions (Zago et al. 2004). A visual target moved vertically downward on a screen with different laws of motion. Subjects were asked to punch a hidden ball that arrived in synchrony with the visual target. They systematically timed their motor responses consistent with the assumption of gravity effects on an object’s mass, both when the visual target was accelerated (1g) and when it moved at constant speed (0g).

Here we used this paradigm to address the question of how the 1g model adapts as a function of the probability of 0g versus 1g targets within one session. This is related to the issue of how humans interact with multiple environments. Concurrent learning of two conflicting environments, such as opposing force fields or opposing visuomotor rotations, has previously been reported to be difficult or very slow, probably because of interference in working memory (Brashers-Krug et al. 1996; Gandolfo et al. 1996; Krakauer et al. 1999). Osu et al. (2004) reported that subjects can learn two opposing force fields when provided with contextual cues and random, frequent switching. However, concurrent learning was slower and more difficult than separate learning. When subjects are exposed to a force field whose amplitude varies randomly from trial to trial, they learn to set their response to the average field experienced over the previous few movements (Scheidt et al. 2001; Takahashi et al. 2001). In a bi-manual manipulation task, when the properties of the manipulated object are randomly changed between trials, the anticipatory modulation of grip force depends on the weighted average of the object’s properties, as experienced over the previous three trials, with the weighting increasing for the most recent trials (Witney et al. 2001). Adaptation to predictably varying environments has also been investigated. Karniel and Mussa-Ivaldi (2002) taught subjects, on separate days, to move in two different velocity-dependent force fields applied at the hand by a robot. Even after this experience, subjects were unable to move accurately when the same two fields alternated after each movement. This suggests that, although subjects can learn and maintain accuracy in both force fields, rapid switching in motor working memory is difficult. A similar conclusion was reached by Wigmore et al. (2002) for visuomotor learning of rotated visual feedback. These studies suggest that computational mechanisms that average across recent trials are used to learn both predictable and randomly varying tasks (Davidson and Wolpert 2003). Thus only short-term memory seems to be used for motor adaptation.

Here we compared five protocols that differed in the probability of 0g versus 1g trials. Intuitively, one would expect that...
the higher the probability of 0g trials and the shorter their temporal distance, the greater the adaptation rate. Indeed, the studies reviewed above indicate effects that tend to decay beyond three consecutive trials. Surprisingly, we found that the adaptation rate to 0g was essentially invariant, bearing no significant relation with the probability or the temporal distance. Adaptation even occurred through very few 0g trials sporadically interspersed during immersive practice with 1g trials. Thus fast learning was event-dependent rather than time-dependent, being linked to the serial repetition of each condition within an experiment.

METHODS

Subjects

Twenty-five healthy subjects (11 women and 14 men; mean age, 29 ± 6 yr) participated in the study. The subjects were right-handed (as assessed by a short questionnaire based on the Edinburgh scale), had normal vision or vision that was corrected for normal, and were naïve to the purpose of the experiments. They gave informed consent to procedures approved by the Institutional Review Board of Scientific Institute Foundation Santa Lucia, in conformity with the Declaration of Helsinki on the use of human subjects in research.

Experimental setup

Setup and general procedures were described in detail in Zago et al. (2004). Briefly, subjects sat on a chair placed in front of a vertical screen (3.94 m wide, 2.13 m high) attached to the ceiling of a dimly illuminated room (Fig. 1). Subjects’ eyes were located at 0.5-m horizontal distance from the screen, 1.82 m below the top. The back of the chair, vertically inclined by 40°, supported the head and torso of the subjects. In that position, subjects could easily reach below and beyond the lower border of the screen by protracting their arm forward. Images were generated by a PC and displayed on the screen by a BARCO Graphics 808s (1,024 × 768 pixels, 85-Hz refresh frequency). A black square box (9 cm wide) was constantly displayed at the top of the screen against white background. In each trial, a red target sphere (9 cm diam) moved vertically downward, emerging from the box, after a random delay ranging from 1.2 to 1.7 s. An auditory signal was followed by the visual target (synchronous timing was determined by means of an optic decoupling unit for safety reasons). All kinematic data were acquired for 5 s, starting 0.4 s before target appearance in synchrony with trial start. Intertrial interval was 14 s. Total duration of each session was 1 h 20 min, with 10 min of rest allowed halfway.

Task

Before the experiment, subjects received general instructions and familiarized with the setup in front of the screen (they could not see behind it). They were told that they should punch a hidden falling ball as it emerged below the lower border of the screen. They were further informed that, to be successful, they had to monitor visually the motion of the sphere on the screen because it arrived at the same time as the hidden ball at the interception point. Between trials, subjects kept a free relaxed posture until an alert auditory signal instructed them to look at the box on the top of the screen and to recoil their arm in the starting posture; with the adducted shoulder, the upper arm was roughly vertical, the forearm horizontal, the wrist mid-pronated, and the hand and fingers clenched in a fist. Because starting position position was not precisely controlled, it could vary somewhat from trial to trial. At trial onset, another auditory signal was followed by the visual target emerging from the box, after a random delay ranging from 1.2 to 1.7 s. Subjects were asked to punch with the finger knuckles so as to deviate the ball trajectory. According to the instructions, a successful interception required contacting any point of the ball with any part of the finger knuckles. Instead, contacting the ball outside the knuckles (such as with the metacarpus, carpus, or forearm) was not counted as a successful trial. Verbal reports provided by the subjects during the

FIG. 1. Experimental setup. Subjects were asked to intercept a virtual sphere moving vertically downward on a screen by punching a real ball that fell hidden behind the screen. Virtual sphere and real ball arrived in synchrony below the lower border of the screen.
experiment attested that they had cognizance of their performance. One experimenter sitting close to the subject kept a written record of performance based on visual impression.

**Protocols**

The visual target descended from the start box with pseudo-randomly assorted initial speeds ($v_{i0} = 0.7, 1, 1.5, 2.5, or 4.5\, \text{m/s}$) and accelerations ($1g = 9.81\, \text{m/s}^2$ or $0g$). The randomization procedure avoided identical conditions in consecutive trials. Each experimental session consisted of blocks of 55 or 50 trials (depending on the protocol) repeated four times consecutively. The probability of a given $v_{i0}$ was always 20% (except for P0 day 1, where the probability of each $v_{i0}$ > 0 was 18% and that of $v_{i0} = 0$ was 9%), but the probability of 0g versus 1g acceleration could vary depending on the protocol and the day of practice. We designed five protocols that differed in the relative probability of 0g versus 1g targets on any given day: P9, P50, P91, P100, and P0 (Table 1). The label denotes the probability ($P$) of 0g targets on day 1. $P$ ranging between 0 (P0) and 100% (P100). Each group included a different set of five subjects, and all subjects of a group were exposed to identical sequences of trials. Subjects of group P50 performed a 1-day experiment with 50% of 0g targets and 50% of 1g targets. In the other groups, there were two experimental sessions 24 h apart. Subjects of group P100 were exposed to an identical sequence of trials on both days, involving only 0g targets (100% probability). Subjects of group P9 were exposed to 9% of 0g targets and 91% of 1g targets on day 1. On day 2, they were exposed to an identical sequence of target $v_{i0}$ but reversed accelerations relative to day 1, resulting in 91% of 0g trials and 9% of 1g trials. On both days, the low probability trials always had the same $v_{i0}$ as the previous trial, but different accelerations. Subjects of group P91 practiced on day 1 (day 2) the same sequence experienced on day 2 (day 1) by subjects of group P9. Thus they had 91% of 0g trials on day 1 and 9% of 0g trials on day 2. The sequence of target $v_{i0}$ was identical for trials at the same acceleration in P9, P91, and P100. Finally, P0 had an identical sequence of trials as P9, except for the low probability trials on day 1, which were all at 1g and $v_{i0} = 0$. In summary, there were 10 randomized conditions (5 initial speeds and 2 accelerations) in all sessions of all protocols, with the following exceptions: on day 1 of protocol P0 there were six conditions (6 initial speeds and 1 acceleration), and on day 1 and day 2 of P100 there were five conditions (5 initial speeds and 1 acceleration).

As a consequence of the different probability of 0g trials, the time interval between any two repetitions of the same target (same acceleration and $v_{i0}$) varied by >10 times across the five protocols. For instance, the time interval between the first and second repetition of target ($0g, v_{i0} = 0.7\, \text{m/s}$) was 1 min 18 s for P100, 1 min 38 s for P91 (day 1), 1 min 45 s for P0 (day 2), 12 min 52 s for P50, and 18 min 1 s for P9 (day 1).

**Data analysis**

**SPATIAL TRAJECTORIES AND MOTOR TIMING.** Spatial trajectories of punching were described by means of the x,y,z coordinates of the arm markers recorded by the Optotrak, after transformation (by translation and rotation) into the reference frame defined by the screen plane (yz) and the orthogonal plane intersecting ball trajectory (xy). Motor timing was quantified from the recorded changes of wrist acceleration, given the high sensitivity and temporal resolution of this signal. Raw data were numerically low-pass filtered (bi-directional 20-Hz-cutoff 2nd-order Butterworth filter) to eliminate impact artifacts (Fig. 2A). We focused on the acceleration component directed along the long axis of the forearm (denoted $a_x$ or wrist acceleration for short), which was available for all experiments. When the three-dimensional components of acceleration were available, we verified that the $a_x$ component was always dominant (>2 times larger than the other 2 components), except at impact with the ball which contributed a large

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**TABLE 1. Protocols**

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<th>Protocol</th>
<th>Day 1</th>
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<td>1g trials</td>
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<td>P9</td>
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<tr>
<td>P0</td>
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**FIG. 2.** Examples of accelerometer recordings (subject A. P.). A: unfiltered (black) and low-pass filtered (red) $a_x$ component of wrist acceleration. Notice that the filter selectively eliminates impact oscillations (the notch around time 0), with no major waveform distortions. B: filtered $a_x$ (red), $a_y$ (blue), and $a_z$ (green) components. Traces are aligned relative to interception time (time 0); negative time is before that time. Acceleration scale in m/s$^2$.

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$a_y$ component (Fig. 2B). Dominance of $a_y$ was due to the small angle (about 10–15°) between the direction of wrist movement and forearm direction (see Fig. 3). We considered three different landmarks on $a_x$ acceleration. The main landmark was represented by the positive peak. In the following, the time of this peak relative to the interception time will be denoted TTC. In addition, we computed the time of zero-crossing as the time when the acceleration first crossed the zero-line after the positive peak, and the time of the negative peak. In correctly intercepted trials, the zero-crossing occurred very close to the interception time (see Fig. 2). This indicates that subjects exerted maximum momentum to punch the incoming ball at the right time, because zero-crossing of acceleration corresponds to peak velocity.

INTERCEPTION SCORE. To provide a global score of performance, we proceeded in the following manner. The time of any measurable contact between the ball and the limb was determined in each trial by the occurrence of specific high-frequency oscillations in the wrist accelerometer signal (see Fig. 2A). To isolate impact oscillations from the lower frequency oscillations due to the voluntary arm movement, the raw signal was filtered with bi-directional 25-Hz high-pass Butterworth filter. Detailed analysis of the combined data set of wrist position and wrist acceleration showed that, when the hand passed close to the expected interception point around the expected interception time, contact oscillations invariably started between the positive peak and the negative peak of acceleration. Therefore we assigned a score of 1 (intercepted ball) to trials in which the contact oscillations started within that interval, and a score of 0 (no interception) if there were no detectable oscillations or they started outside the interval. For instance, the trial plotted in Fig. 2 was scored 1. In general, there was

**FIG. 3.** Spatial trajectories of punching. Arm trajectories in the sagittal plane plotted for a representative subject (M. A., protocol P0, $v_0 = 0.7 \text{ m/s}$), as seen from his right side. A: path described by shoulder, elbow, and proximal and distal wrist markers is superimposed on a schematic arm. Red sphere indicates theoretical position of the ball at interception time. B and C: trajectories of distal wrist marker in 40 $1g$ trials and 40 $0g$ trials, respectively. D and E: 1st (red traces) and last (blue traces) repetitions from the set of trials of B and C, respectively. In all panels, trajectories are plotted from start time to interception time. Tick marks on x- and y-axes are placed every 20 cm.
good agreement between the score assigned by this procedure and the score assigned by the experimenter based on visual impression (see Task). Only the former was used for quantitative analysis. For each protocol, global interception score was computed as the fraction of all intercepted trials out of the total number of trials (over all subjects of a given group) of all \( v_0 \) for a given acceleration.

**ADAPTATION RATE.** An exponential function was fitted to the series of repetitions of the chosen parameter \( \xi \) (e.g., TTC or score) to characterize the rate at which subjects adapted during an experiment. The function has three free parameters: offset \( b_0 \), gain \( b_1 \), and learning-constant \( b_2 \). The general equation was

\[
\xi_i = b_0 + b_1 \exp(-i/b_2)
\]

where \( \xi_i \) was the \( \xi \) value estimated for repetition \( i \).

**STATISTICS.** Few trials (<0.1% of all trials) were excluded from the analysis due to the presence of artifacts or lack of subject’s attention during the trial as marked in the experimenter notebook. Differences between conditions were assessed using single- or multiple-factor ANOVA. The threshold for statistical significance was set at \( \alpha = 0.05 \). Statistically significant differences of interception scores between experimental conditions were assessed using Pearson \( \chi^2 \). Statistics on correlation coefficients was performed on the normally distributed, Z-transformed values (Kendall and Stuart 1969).

**RESULTS**

**Spatial trajectories**

Punching movements recorded by the Optotrak system mainly occurred in the sagittal plane (xy) intersecting ball trajectory, orthogonal to the projection screen (yz). At interception time (time of synchronous arrival of the virtual target and of the real ball), the intrtrial variability of wrist position outside the sagittal plane was limited: the mean of the \( z \) coordinate of wrist position was 1.7 \pm 4.9 (SD) cm across all subjects (\( n = 25 \)). Figure 3A shows the path of the arm markers in the sagittal plane for a typical intercepted trial. Trajectories have been plotted from the start time up to the interception time. Arm configuration and position of the ball at the interception time are schematically indicated.

Trajectories of the most distal marker are superimposed for 40 trials with the visual target (\( v_0 = 0.7 \text{ m/s}, 1 \text{g acceleration} \)) and 40 trials (\( v_0 = 0.7 \text{ m/s}, 0 \text{g acceleration} \)) in Fig. 3, B and C, respectively. Note that in this experiment (group P0), 1g trials were performed the day before 0g trials. Markers’ placement was similar but not necessarily identical between days. In general, punching involved the protraction of the hand forward and slightly upward. Most movements directed to 1g targets arrived at the interception zone at the right time. In this subject, the mean distance of the wrist marker from the theoretical position of the ball was 12.1 \pm 4.1 (SD) cm (\( n = 40 \) repetitions) at interception time. This distance corresponds to the distance between the wrist marker and the finger knuckles when the hand is clenched in a fist, where contact with the ball occurred in successful interception. The variability of the endpoint (SD of xy wrist position) can be accounted for by two sources. 1) Physiological variability. According to the instructions given to the subjects, contact between any part of the finger knuckles and any point of the ball represented a successful interception, resulting in a potentially wide spectrum of hand geometries compatible with interception. 2) Measurement variability. The accuracy of the estimate of the position of the wrist marker at interception time was mainly limited by our sampling rate at 200 Hz (see methods). Because punching speed was high, temporal limitation translated in spatial uncertainty. For the data of Fig. 3, the peak tangential velocity of the wrist (occurring around interception time for 1g trials, see Motor timing) was 4.1 \pm 0.4 (SD) m/s, yielding a spatial uncertainty of about \( \pm 2 \) cm at that time.

In contrast with the movements directed to 1g targets, those directed to 0g targets (Fig. 3C) arrived well beyond the interception zone at interception time. In other words, the hand passed through the interception zone too soon. For many 0g trials, subjects failed to punch the ball, and they were hit by the ball at the metacarpus, the carpus, or even the forearm. At interception time, the mean distance between wrist position measured in 0g trials and that measured in 1g trials was 17.3 \pm 7.3 (SD) cm (\( n = 40 \) repetitions). With practice, however, there was some improvement of performance. Figure 3, D and E, shows the first (red traces) and the last (blue traces) repetitions of the trials plotted in Fig. 3, B and C, respectively. The wrist position at interception time did not differ substantially between the two 1g repetitions (Fig. 3D). Instead, the wrist movements were markedly different between the two 0g repetitions (Fig. 3E). In the first repetition, the hand arrived too soon at the interception zone and slowed down with an upward curl. In the last repetition, the hand was much closer to the correct position at the right time and did not wind up. The distance between the wrist positions at the interception time in these two trials was 9.1 cm. Nevertheless, the wrist was still too anterior in the last 0g repetition. In the subject of Fig. 3, there were other differences between movements directed to 1g targets and those directed to 0g targets. Movements to 1g targets progressed monotonically forward, from the start position to the interception zone (although the starting position varied somewhat across trials). Movements to 0g targets sometimes involved a brief recoil of the arm backward (see the hooks on the left end of traces of Fig. 3C), followed by the forward protraction of the arm. However, these differences were not systematic across subjects.

Verbal interview with the subject at the end of the experiment revealed that, during the experiment, he was well aware of the mistakes he made. He declared that he had strived to reach the level of performance of the day before, but that he failed for reasons unknown to him. He simply described these trials as more difficult. Similar reports were obtained by all other subjects.

**Motor timing**

Analyses of the waveforms recorded by the wrist accelerometer at high temporal resolution (1 ms) allow an accurate description of the timing of the motor responses. The time course of the changes of wrist acceleration is plotted in Fig. 4 for the same trials of Fig. 3. Traces are aligned relative to the interception time. Negative (positive) values indicate times before (after) that time.

As one would expect from the previous analysis of spatial trajectories, the motor responses to 1g targets (left) were timed very differently from those to 0g targets (right). Motor responses to 1g targets were closely time-locked to the interception time (time 0 on the abscissa) from the first repetition and varied little in the following repetitions. On average, wrist acceleration reached the positive peak at \( -45 \pm 10 \) (SD) ms (\( n = 40 \) repetitions). The zero-crossing occurred at 2 \pm 10 (SD) ms, indicating that subjects generated maximum momentum to punch the incoming ball at the right time. After the
punch, the hand movement was rapidly braked. The negative peak of acceleration occurred at 42 ± 11 (SD) ms.

In contrast, the responses to 0g targets tended to start and to end too early. In the first repetition of Fig. 4, the positive peak, the zero-crossing, and the negative peak occurred at −221, −181, and −142 ms, respectively. The entire acceleration waveform for this 0g trial was shifted earlier in time relative to that of the waveform for 1g trials by about 180 ms. Thus the hand arrived too soon at target destination and slowed down passing through and beyond the interception zone (see Fig. 3E). With practice, subjects tended to improve the timing of 0g responses, but the responses often remained premature compared with 1g responses. In the last repetition of Fig. 4, the positive peak, the zero-crossing, and the negative peak occurred at −59, −17, and 25 ms, respectively. Thus the acceleration waveform for this 0g trial was anticipated in time relative to that of the waveform for 1g trials by about 17 ms. Notice also the greater variability (jitter) in timing of 0g trials compared with 1g responses.

In contrast with the timing, the shape of wrist acceleration waveforms depended much less on the law of target motion, although it was not necessarily invariant across trials. In general, the positive component of the acceleration profiles changed little across trials and conditions. However, in some 0g trials, this component was slightly prolonged, reflecting slight hesitancies of the movement. The negative component tended to be slightly more pronounced in amplitude for 0g trials than for 1g trials, indicating a stronger effort to brake the movement.

To quantify the temporal relationship between different landmarks of wrist acceleration as a function of target acceleration, we computed the time interval between a given landmark in each 1g trial and the same landmark in the corresponding 0g trial. Thus ΔPP was the time interval between the positive acceleration peak in each 1g trial and the same landmark in the corresponding 0g trial, whereas ΔZC was the time interval between the zero-crossing in the 1g trial and the same landmark in the 0g trial. When the data of all experiments (P9, P50, P91, P0) were pooled together (n = 3,455), they appeared scattered through a wide range because the timing of the responses varied across 0g trials (see Fig. 4). Importantly, however, the best-fitting regression line of ΔZC versus ΔPP (r² = 0.87; intercept, −0.6 ms; slope, 0.98) was similar to that one would expect if the landmarks on the acceleration waveform maintained the same temporal relationship in 0g and 1g trials. Moreover, the time interval between the positive peak of hand acceleration and the zero crossing of each acceleration trace varied little across all conditions (by pooling all trials of all subjects, the mean SD was 17 ± 2 ms).

In addition, the temporal landmarks of wrist acceleration were reasonably good predictors of the wrist position measured
at interception time. Thus the $r^2$ between the time of the positive acceleration peak and the horizontal (vertical) coordinate of the wrist marker was 0.66 (0.71) for the data of Figs. 3 and 4. In other words, the earlier was the time of occurrence of the positive acceleration peak, the farther did the hand move relative to the interception zone. One would not expect a higher correlation than that reported, given 1) the intertrial spatial variability noticed above and 2) the non-unique mapping between acceleration profile and wrist path. In the following, we will concentrate on the time of occurrence of the positive peak relative to the interception time. This time will be denoted TTC, considered as a reliable motor correlate of the time-to-contact of the target estimated by the subject. However, we will show that the main results are similar if one uses a different temporal landmark of the acceleration trace. In addition, we will report the results obtained with an independent estimator of performance, the interception score.

The aim of this paper was to address the issue of whether learning to time the motor responses depends on the relative probability of 0g versus 1g targets, and on the time interval between successive repetitions of the same target during each experiment. To this end, we first present the results for each different protocol separately and then compare the results across all protocols.

**Protocol P9**

On day 1 of protocol P9, 91% of visual targets moved at 1g, and 9% randomly interspersed targets moved at 0g. The mean TTC values (averaged across all subjects, $n = 5$) are plotted as a function of the repetition number separately for each initial speed in Fig. 5 (filled and empty symbols correspond to 1 and 0g trials, respectively). On average, the TTC was $-49 \pm 25$ (SD) ms (across all trials at all initial speeds of 5 subjects, $n = 995$) for these immersive 1g trials. Two-factor ANOVA showed no significant effect of repetition ($P = 0.3$) and border-line effect of initial speed ($P = 0.07$) on these TTC values. The effect of speed was non-monotonic. The random occurrence of sporadic 0g trials did not affect the performance for subsequent 1g trials. In particular, the TTC of the 1g trial following a 0g trial did not differ significantly ($P = 0.13$) from the TTC of the previous 1g trial with the same $v_0$.

In the first presentation of each condition ($v_0$) of sporadic 0g targets, subjects missed the targets by a large amount. On average, TTC was $-217 \pm 88$ (SD) ms (across the 1st presentations of 0g trials of 5 subjects, $n = 25$), that is 168 ms earlier than the mean TTC of 1g trials of the same day. However, at each successive presentation of a given 0g condition the response generally improved over the previous presentation of the same condition, despite the relatively long time interval (about 20 min) separating these events (corresponding to 55 trials). On average, the TTC of the second presentation of all 0g trials (except those for $v_0 = 4.5$ m/s) was closer to the interception time than that of the first presentation by $68 \pm 12$ (SE) ms (across all subjects and $v_0 < 4.5$ m/s, $n = 20$), and the following responses were further shifted toward correct values. Instead, the responses at $v_0 = 4.5$ m/s did not vary significantly across the four repetitions. TTC of 0g trials was significantly dependent on both repetition ($P < 0.001$) and $v_0$ ($P < 0.05$, 2-way ANOVA): TTC was shorter (closer to interception time) with both increasing $v_0$ and repetition.

On day 2, the same group of subjects was trained with a series of trials that was the mirror image of day 1 in so far as target acceleration was concerned: 91% of 0g trials and 9% of 1g trials. Surprisingly, all subjects showed retention of the 0g conditions, despite their sporadic occurrence on day 1 and no additional practice between the 2 days. For any given $v_0$, the TTC of the first 0g trial of day 2 was not significantly different from the corresponding value of the last (4th) 0g trial with the same $v_0$ of day 1 (paired t-test, $P = 0.38$). On the other hand, the TTC of the first 0g trial of a given $v_0$ on day 2 was significantly higher (paired t-test, $P < 0.05$) than that of the first 0g trial of the same $v_0$ on day 1 (except for $v_0 = 4.5$ m/s).

The most important finding of this experiment is given in Fig. 5, right panels, one recognizes a clear exponential trend of TTC with repetition. Parameters of exponential fitting (Eq. 1) are listed in the figure legend. Notice that,
even at the end of immersive 0g training on day 2, the performance remained significantly poorer than that with 1g trials on day 1. Mean TTC over the last three repetitions of 0g trials at each \( v_0 \) of day 2 was \(-95 \pm 44 \, \text{(SD) ms} \) \((n = 75)\), which is 46 ms earlier than the mean TTC of 1g trials of day 1.

On day 2, the random occurrence of sporadic 1g trials did not affect the performance for subsequent 0g trials. Thus the TTC of the 0g trial following a 1g trial did not differ significantly from the TTC of the previous 0g trial with the same \( v_0 \). However, the sporadic 1g trials were associated with significant aftereffects. The 1g trials of day 2 are plotted adjoined with those of day 1 in the left panels of Fig. 5. For each \( v_0 \), TTC of the four 1g trials of day 2 were significantly \((P < 10^{-8})\) delayed with respect to TTC of the last four 1g trials of day 1 (on average by \(22 \pm 14 \, \text{(SD) ms}, n = 20\)). Also the TTC of sporadic 1g trials on day 2 did not depend significantly on speed or repetition, as was the case for the immersive 1g trials on day 1.

**Protocol P50**

This was a 1-day protocol with 50% of visual targets at 0g and 50% of targets at 1g, initial speed and acceleration being randomized from trial to trial. Three-way ANOVA showed that TTC of 1g trials (Fig. 6, ○) did not depend significantly on repetition \((P = 0.3)\) or \( v_0 \) \((P = 0.1)\), but they depended significantly \((P < 0.005)\) on the acceleration of the preceding trial. When the preceding trial was 0g, TTC was slightly delayed (on average, by 7 ms) relative to when it was 1g.

TTC of 0g trials (Fig. 6, ●) depended significantly on repetition \((P < 0.01)\), \( v_0 \) \((P < 10^{-6})\), and on the acceleration of the preceding trial \((P < 0.005, 3\)-way ANOVA\). When the preceding trial was 1g, TTC was slightly anticipated relative to when it was 0g. With practice, TTC values of 0g trials became closer to the interception time for all \( v_0 \), following an exponential function (see figure legend).

**Protocol P91**

For this and the next two protocols, the mean TTC values are plotted for \( v_0 = 0.7 \) and 1 m/s in Fig. 7, and the data for the other speeds are described in the text. P91 was the reverse of P9. On day 1, there were 91% of 0g trials and 9% of 1g trials, whereas on day 2, there were 91% of 1g trials and 9% of 0g trials (Fig. 7, top). On day 1, the TTC of immersive 0g trials shortened exponentially as a function of repetition (see figure legend). Mean TTC of the sporadic 0g trials of day 2 was significantly \((P < 0.05)\) earlier than mean TTC of the last four 0g trials of day 1 for \( v_0 = 0.7 \, \text{m/s} \), whereas the difference was not significant for all the other \( v_0 \). Mean TTC of 0g trials of day 2 was significantly \((P < 0.05)\) closer to interception time than mean TTC of the first 0g trials of day 1. TTC of 0g trials of day 2 did not depend significantly on repetition for all \( v_0 \) except for \( v_0 = 1 \, \text{m/s} \). In the latter condition, the TTC of the first 0g trial was significantly earlier than the mean TTC of the last four 0g trials of day 1 \((P < 0.005)\), but already the TTC of the second 0g trial became not significantly different from the last four 0g trials of day 1.

On day 2, the TTC of immersive 1g trials was time-locked to the interception time from the beginning of the session, and it did not depend significantly on repetition (ANOVA, \( P = 0.9 \)) or speed \((P = 0.6)\). Instead, the TTC of sporadic 1g trials randomly presented on day 1 was significantly delayed relative to the TTC of the first four 1g trials of day 2 for \( v_0 > 0.7 \, \text{m/s} \), indicating the existence of aftereffects during immersive practice with 0g trials on day 1. Also, the TTC of sporadic 1g trials did not depend significantly on speed or repetition, as the TTC of immersive 1g trials.

**Protocol P100**

Here subjects were presented with 100% of 0g targets in the same sequence over the 2 days. As in the other protocols, the responses were timed too early (Fig. 7, middle). On day 1, TTC shortened exponentially as a function of repetition (see figure legend). On day 2, the TTC values changed little throughout
the session, and remained similar to the corresponding values measured at the end of day 1. Thus for each $v_0$, TTC of the first four repetitions of day 2 was not significantly different from that of the last four repetitions of day 1, nor was it significantly different from that of the last four repetitions of day 2. Even at the end of 0g training on day 2, responses remained premature: mean TTC over the last four repetitions of 0g trials at each $v_0$ of day 2 was $-127 \pm 73$ (SD) ms ($n = 100$).

Protocol P0

In the protocols reported so far, subjects were exposed to 0g trials from the first session. As the greatest part of learning occurred in the first session, general practice with the punching task might have contributed to the fast 0g learning. To address this point, we modified the previous version of P9. The sequence of trials was the same as in P9, but the sporadic 0g trials of day 1 were replaced by sporadic 1g trials with $v_0 = 0$ (Fig. 7, bottom). In this manner, 0g trials were presented on day 2 only. We found that the TTC of immersive 1g trials of day 1 with $v_0 > 0$ were time-locked to the interception time, as were the TTC of the sporadic 1g trials with $v_0 = 0$ of the same day. TTC of these latter trials did not differ significantly from the TTC of the preceding trial. When subjects were exposed to 0g trials on day 2, they exhibited a trend similar to that described in the other protocols. In particular, TTC changes with repetition were fitted by a double-exponential in the condition $v_0 = 0.7$ m/s and by a single-exponential for $v_0 = 1$ m/s (see figure legend), as in the two adjoined sessions of P9. As in the previous protocols, 0g learning was associated with significant aftereffects when sporadic 1g trials were randomly presented on day 2.

Covariance of changes of different temporal landmarks

The results reported above were qualitatively the same independent of the temporal landmark of wrist acceleration that was chosen to describe motor timing. Figure 8 plots the values of time of occurrence of positive peak (TTC, blue), zero-crossing (red), and negative peak (green) for the condition $v_0 = 1$ m/s in group P9 (top) and group P100 (bottom). All these temporal landmarks covaried tightly across repetitions for both 1 and 0g trials. Similar results were found for all conditions of all protocols. The $r^2$ between each pair of landmarks across all trials was always $>0.90$.

Interception score

The timing (TTC) of the wrist acceleration peak reflects the estimate of the target time-to-contact made by the subject. The success in the task depends on global spatiotemporal coordination of the punching movement: this must intercept the trajectory of the falling ball at the right time and place. For each protocol, we computed the interception score for any given repetition as the fraction of intercepted trials of all five $v_0$ of all five subjects (Fig. 9). Only the results for high probability ($\geq 50\%$) trials are presented in the figure, except for the 0g trials of day 1 of P9, which are plotted adjoined to those of day 2 (Fig. 9, red, right panel).

The overall trend is similar to that previously described for TTC. For P9, P91, and P0, the interception score of 1g trials was high from the outset and improved only slightly with practice (Fig. 9A). On average, it was $85 \pm 5\%$ in the first four repetitions and $92 \pm 7\%$ in the last four repetitions (paired $t$-test on the difference, $P = 0.23$). In P50 (green trace), instead, the interception score was initially much lower than in the other protocols ($49 \pm 11\%$ over the 1st 4 repetitions) and tended to increase significantly ($r = 0.68, P < 0.01$) with repetition, reaching values comparable to those of the other protocols after about 15 repetitions.

In all five protocols, the interception score of 0g trials was very low in the first repetition (14 $\pm 11\%$) and tended to increase exponentially with repetition (Fig. 9B). Even at the end of practice, the score was significantly ($P < 10^{-3}$) lower.
than that in 1g trials (on average, it was 59 ± 13% over the last 4 repetitions).

The interception score for the 1g trials was significantly (P < 10⁻⁶) lower when they occurred as low probability (9%) trials (catch trials) than when they occurred as high probability (91%) trials. When the results from all repetitions and protocols were pooled together, the mean score was 38 ± 20% in the former case and 88 ± 9% in the latter case.

Comparison of 0g learning across protocols

Adaptation rate. The changes of behavior that occurred at the beginning of practice reflect the rapidity with which subjects adapted. This component of 0g learning was very similar across protocols, whether it was assessed for interception score, TTC, or the other temporal landmarks. On average, the learning-constant (b₂ in Eq. 1) of the exponential fit was 1.53 repetitions for interception scores and 1.57 for TTC. Because about 90% of adaptation occurred by the fourth repetition of a given 0g condition, further quantitative analysis was carried out on the first four repetitions.

To facilitate visual comparison across protocols, the changes of interception scores over the first four repetitions (marked against orange background in Fig. 9B) have been replotted in Fig. 9C after being offset by a constant equal to the distance between the group mean and the general mean. Clearly, the rates of change of interception scores are very similar across protocols, as are the learning constants of the exponential fit as a function of repetition (see figure legend). ANOVA showed that the difference between the interception score of the fourth and that of the first repetition does not depend significantly on protocol (P = 0.96). Comparable results were obtained with TTC. Two-factor ANOVA on the learning constants of the exponential fit of TTC showed that they do not depend significantly on either protocol (P = 0.65) or speed (P = 0.64).

Behavioral parameters have been plotted so far as a function of repetition number, ignoring their relationship with the real-
time of occurrence of each event. Figure 10 presents the data on a time scale. Step changes in TTC of the first four repetitions of target 0g, \( v_0 = 0.7 \text{ m/s} \) are plotted as a function of the time elapsed between presentations in each protocol. The bottom panel shows the mean ± SD difference between the TTC of the fourth and first repetition of the same target, plotted as a function of the time elapsed between these two presentations in each protocol. The TTC increment did not change significantly over this wide range of time intervals (ANOVA, \( P = 0.98 \)), nor did it change significantly as a function of the time interval between any two consecutive presentations of 0g targets, independent of their speed. Similar results were found for TTC of the first four repetitions of target 0g, \( v_0 = 1 \text{ m/s} \) (ANOVA, \( P = 0.32 \)).

Therefore we conclude that the rate of fast 0g learning depends on the serial repetition of a condition within the experiment and does not depend on the time interval between successive repetitions.

OFFSET IN PERFORMANCE. The offset values of interception score and TTC measured at the beginning and end of practice reflect the overall level of performance, independent of the intervening rate of change. Offset values were computed as the mean values either over the first four repetitions or over the last four repetitions. These values did vary across groups, although we cannot rule out interindividual differences. In general, the performance tended to rank from high to low in the following order: P0, P9, P50, P91, and P100. Thus mean TTC over the last four repetitions for the condition \( v_0 = 0.7 \text{ m/s} \) was \(-68, -95, -103, -154, \) and \(-173 \text{ ms} \), respectively (for reference, TTC of 1g test trials was about \(-50 \text{ ms} \)). The trend was similar, although nonmonotonic, for the other offset values. They were significantly related to protocol (ANOVA, \( P < 0.002 \)).

It is clear that this ranking of performance has nothing to do with the probability of 0g trials on the day in which steady-state performance is assessed: thus P0, P9, and P91 all had 91% probability of 0g trials on that day, but differed widely in terms of steady-state performance. Instead, the above ranking covaries with the probability of 1g trials on the first experimental day: 100% in P0, 91% in P9, 50% in P50, 9% in P91, and 0% in P100. In other words, the higher the previous exposure to 1g targets, the better the steady-state performance with 0g targets. Obviously, the ranking covaried in the opposite direction with the probability of 0g trials on the first experimental day, although it seems counterintuitive that the steady-state performance with 0g targets is worse in case of a higher previous exposure to 0g targets.


discussion

Current evidence indicates that the construction and consolidation of a new internal model involves time-dependent processes (Shadmehr and Brashers-Krug 1997), but event-related components have also been shown (Witney et al. 2000). Several previous studies have shown that subjects can learn and consolidate in memory opposing force fields or opposing visuomotor rotations when they are trained in each task separately, with a sufficiently long time interval between each training session (Brashers-Krug et al. 1996; Krakauer et al. 1999; McGonigle and Flook 1978; Shadmehr and Brashers-Krug 1997). Anterograde and retrograde interference prevent learning and consolidation of a new internal model when the two conflicting environments are practiced within 5 min to 6 h. Osu et al. (2004) reported that subjects can adapt simultaneously to two opposing force fields when provided with contextual cues and can consolidate motor memory if random and frequent switching occurs. However, simultaneous learning was slower and more difficult than separate learning. It has been suggested that humans can adapt to two conflicting environments not merely by using feedback control but at least
partly through simultaneous acquisition of multiple internal models and their predictive switching (Ozu et al. 2004; Wolpert and Kawato 1998). Learning and decay of an internal model may have different time courses. Thus in a bi-manual manipulation task, anticipatory responses are quick to develop but when they become inappropriate they decay slowly, with a rate of decay that depends on the number of trials since the last appropriate event rather than time (Witney et al. 2000).

Here we studied how subjects learn to deal with two conflicting sensory environments represented by 1g and 0g visual targets. We found that the adaptation rate to 0g was essentially invariant across protocols, with no significant relation with the probability or the temporal distance between identical targets. Thus initial learning was event-related rather than time-related, being linked to the serial repetition (1st, 2nd, etc.) of a 0g target within an experiment. The tasks we studied differ in some important respects from those reviewed above. First, both the responses to 1g and 0g trials were compatible with the internal gravity model. The 1g model presumably is pre-existent, as indicated by the observation that performance with 1g targets was generally quite good from the beginning of training and improved only slightly afterward, except in P50, where improvement was more marked. Instead the responses to 0g targets were always premature and improved significantly with repeated presentations with a fast learning constant that was independent of the specific protocol.

Although 0g learning was not prevented by concurrent training with 1g, these two tasks were not independent. In fact, we observed interference in the protocol P50 where 0g and 1g trials were equiprobable: the interception score for 1g targets was significantly lower than in the other protocols in the first part of the experiment, and TTC of both 0g and 1g trials depended significantly on whether the preceding trial was 1 or 0g. Interference decreased with practice, as shown by improvement of performance for both 0g and 1g trials. Also, catch trials may reveal the presence of aftereffects due to adaptation of an internal model. In previous studies, catch trials usually consisted of the unexpected removal of a perturbed condition during immersive practice with the perturbation (Shadmehr and Mussa-Ivaldi 1994). Here, low probability (9%) 1g trials exhibited significant aftereffects during immersive 0g practice, the responses being systematically delayed with no trend with repetition. The responses to low probability (9%) 0g targets during immersive 1g practice were systematically anticipated, but there was a consistent learning trend with repetition.

Further evidence that the performance with the two target accelerations was not independent is provided by the finding that the steady-state performance with 0g targets was roughly proportional to the probability of 1g trials on the first experimental day. This result may depend on long-term effects of calibration of the 1g model: the greater the previous exposure to 1g targets, the greater the subsequent extent of steady-state adaptation to 0g targets.

Practice with a novel environment may lead to formation of the appropriate internal model, and multiple internal models specific for individual objects could be stored in motor memory. However, while we experience many different types of objects, normally we experience only one gravity level on earth. Adaptation of a single gravity model would be the most parsimonious solution to deal with variable drag effects. Vertical motion of objects is accelerated by gravity and decelerated to a variable extent by air (or other fluid) friction depending on the object’s mass, size, shape, texture, and fluid viscosity, but falling objects seldom reach constant velocity. The required adaptation is generally more limited than that involved by these experiments, and should be much more successful.

These findings are compatible with the hypothesis that, with 0g training, the 1g model was not switched off, but adapted by shifting the time of motor activation (Zago et al. 2004). Evidence against the hypothesis that the 1g model was not switched off to rely entirely on visual information to estimate target TTC is provided by the aftereffects of sporadic 1g targets during immersive 0g practice. Evidence that the 1g model was not fully replaced by a new 0g model is provided by the systematic residual errors even at the end of extensive 0g practice. Also, we can exclude that these errors depend on the nature of the visual targets employed. It is well known that human vision discriminates more precisely constant speed motion than accelerated motion (Werkhoven et al. 1992). Therefore one would expect a better performance with 0g targets than with 1g targets. Indeed, we previously showed that when the same 0g visual targets used here are intercepted virtually by clicking a mouse-button in the absence of the real ball, the responses are correctly timed (see Fig. 12 in Zago et al. 2004). Thus it is the task of punching a real (although hidden) ball that calls into play an internal model of the effects of gravity on an object’s mass. On the other hand, we cannot rule out the possibility that, here, subjects learned to use a combination of two distinct internal models, the original 1g model and a new 0g model, the relative weight of each one changing as a function of the context.

The fast learning constants of adaptation we found are very similar to those reported for catching tasks involving adaptation of muscle activity to a change of either the height of fall of the ball (see Fig. 7 in Lacquaniti and Maioli 1989a) or the mass of the ball (see Fig. 3 in Lang and Bastian 1999), as well as point-to-point elbow movements suddenly perturbed by an external load (Weeks et al. 1996). In those previous studies, the mechanical oscillations of the arm resulting from ball impact on the hand were damped out more effectively starting from the second trial of practice with a given condition. Thus the 1g model could be used not only for timing a motor action but also for controlling the overall arm impedance. These results pertain to interception of vertical motion. It remains to be seen whether people use a different internal model in case of target motion along directions different from the vertical.

A surprising result was that, at each successive presentation of a low probability 0g target during immersive 1g practice on day 1 of P9, the responses generally improved over the previous presentation of the same condition, despite the relatively long time interval (about 20 min) separating these events. To our knowledge, this is the first evidence that humans can learn and remember a motor task with catch trials. However, our subjects did not merely learn about the existence of catch trials, but developed genuine adaptation to 0g. In fact, we did not observe any comparable learning with 1g-catch-trials during immersive 0g practice (day 1 of P91 and day 2 of P9 and P0). Moreover, when the TTC values of the low probability 0g trials of day 1 of P9 were adjoined to the TTC values of the 0g trials of day 2, we found an exponential trend with repetition very similar to that found in the other groups in which 0g trials were presented with a much higher frequency. Not only did low
probability 0g trials show adaptation, but also they were sufficient to start consolidation in long-term memory as shown by retention 24 h later in P9, to the same extent as after fully immersive training with 0g trials (P100).

A discussion about the mechanisms underlying the described form of motor learning can only be speculative. Event-related learning cannot readily be explained in the context of the known differences between massed and spaced training. Massed training, whereby stimuli are given one after the other without rest, tends to determine robust short-term memory but mediocre long-term memory. In contrast, spaced training tends to be more effective than massed training in producing long-term memory (Scharf et al. 2002). Here both short-term (of the order of minutes) and long-term (24 h) effects seemed independent of the time spacing between consecutive repetitions of each target. The behavioral changes (interception timing and score) associated with 0g repetitions did not have the all-or-none or digital nature of episodic memory, but were gradual and incremental, building on top of the state acquired in the previous repetition of the same condition until saturation. This form of event-related learning implies that the internal store does not decay rapidly, but can be sustained for variable periods between 1 and 20 min after the previous target presentation (Fig. 10). This is compatible with a multiple-stage memory mechanism, with exponential rise and decay in the initial stages followed by a sample-and-hold module. The output of the sample-and-hold would furnish the level of the internal store. Reverberation of activity in a collection of excitatory neurons or synaptic potentiation, both lasting longer than 20 min, may account for a sample-and-hold memory. Attentional and motivational states, such as those required by interception tasks, are known to be accompanied by increased monoaminergic and cholinergic transmission at different brain sites, facilitating induction of the early stage of synaptic plasticity (early long-term potentiation/long-term depression) promoted and sustained by autophosphorylation activity of specific protein kinases (Huang and Kandel 1996; Huerta and Lisman 1995; Lisman et al. 2002). Monoaminergic transmission also plays a pivotal role in the transition between early and long-term plasticity, a process that requires novel protein synthesis through activation of CREB-like transcriptional factors and believed to subtend memory consolidation (Huang et al. 1994; Martin et al. 2000). Because two or more waves of protein synthesis have been shown to exist during the consolidation period, they also might contribute to the sample-and-hold mechanism we have hypothesized.

In summary, we provided evidence for a form of motor learning that is event-related rather than time-related. Learning independent of the probability of alternative events departs prima facie from probabilistic models of sensorimotor learning (Kording and Wolpert 2004). However, the special nature of the internal model of gravity, as of other environmental invariants, should be taken into account. The bias toward the a priori of earth gravity predominates in the central estimates of environmental forces when we deal with real objects (McIntyre et al. 2001; Zago et al. 2004).

We surmise that event-related learning, being highly efficient, might be more frequent than it is usually thought. One would expect this in situations where single events are of potential major significance, so that their impact on adaptation is commensurate to their importance. For instance, when we play a tennis or badminton match, timing errors in handling a drop shot are probably remembered until the next such shot, independent of the time elapsed between the two events.

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