Does the brain model Newton's laws?

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How does the nervous system synchronize movements to catch a falling ball? According to one theory, only sensory information is used to estimate time-to-contact (TTC) with an approaching object[1,2]; alternatively, implicit knowledge about physics may come into play[3,4]. Here we show that astronauts initiated catching movements earlier in 0 *g* than in 1 *g*, which demonstrates that the brain uses an internal model of gravity to supplement sensory information when estimating TTC.

An intuitive means of estimating TTC with an approaching object is to divide the object's distance (d) by its velocity (v). For an object approaching along the sight line, the ratio (τ) of the size of the object's retinal image (r) to its rate of change (dr/dt) is equivalent to the first-order estimate of TTC (d/v) (ref. 2). The CNS could trigger anticipatory actions when τ reaches a certain threshold, using only the visual signals r and dr/dt (refs. 2, 5). Because motor responses could be geared to sensory signals alone, strategies based on first-order estimates of TTC or its inverse[5–10] fit well the Gibsonian theory of ecological perception[1,2,10].

First-order mechanisms suggest attractively simple neural implementations, but provide exact TTC estimates only for constant velocity motion. Although it has been argued that resulting errors may be tolerable when intercepting an accelerating object[5], a strategy that includes both acceleration and velocity (a second-order estimate) could tackle a wider range of behaviors with greater precision. However, as the human visual system is a poor discriminator of acceleration (especially over short time windows[11]), it is difficult to account for arbitrary accelerations of the target. Nevertheless, some specific accelerations, such as gravity, can be foreseen based on simple physics. Thus, when catching a ball, presupposed knowledge

about the most likely path and law of motion may be used[3]. By using an internal model of gravity, the human nervous system could account for the acceleration of a falling object and more accurately predict TTC[3,12].
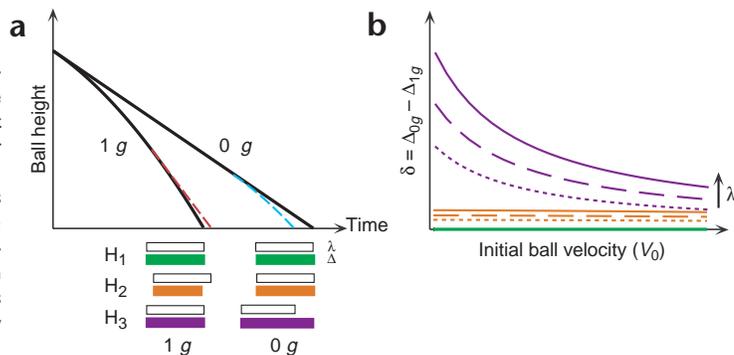
The hypotheses described above predict systematic differences in the timing of catches when the accelerating effects of gravity are removed (**Fig. 1**). In this respect, the 17-day Neurolab space shuttle mission provided a unique opportunity to test these hypotheses. Subjects caught a 400-gram ball that was projected downward with one of three randomly assorted initial speeds (0.7, 1.7 and 2.7 m/s) from a starting point 1.6 m above their outstretched hand. Four subjects performed the experiment 3 times before the flight (90, 30 and 15 days before launch), 3 times during the flight (flight days 3, 9 and 15), and 6 times after the flight (0, 1, 2, 5, 9 and 15 days after return to Earth). Two additional subjects performed the experiment once during the flight and at least once on the ground.
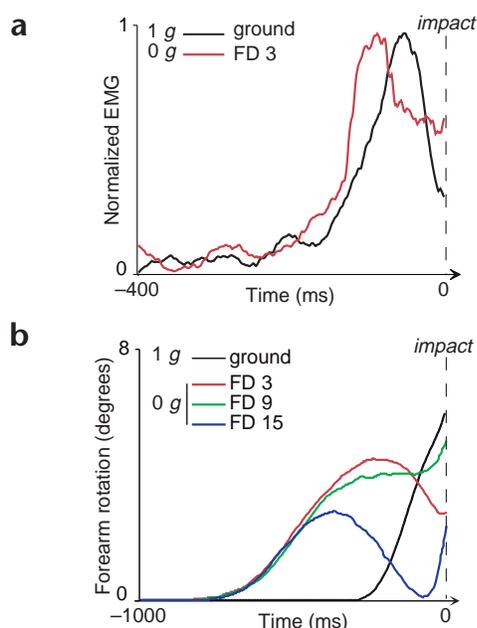
On Earth, catching responses were well synchronized with the arrival of the ball, in agreement with previous findings[3,6,12]. Subjects rotated their forearm upward approximately 200 ms before contact with the ball, with little variability across trials or test days (intra-subject s.d., ± 29 ms). The stiffness of the limb was also increased just in time for impact by a peak of muscle activity (EMG) that, in the biceps, occurs 40 ± 9 ms before impact, independent of the initial ball speed.

In 0 *g*, the peak of anticipatory biceps EMG occurred earlier (relative to impact) as compared to 1 *g* (**Fig. 2a**). This shift was not due to practice, as the timing was restored to pre-flight values upon return to Earth. Nor could it be explained by the longer time it takes the ball to travel the same distance in 0 *g* for the same initial velocity—changing drop heights on Earth so as to match the drop durations used during the flight led to no statistical differences in timing. Furthermore, the constant timing of EMG versus impact on the ground argues against a fixed distance threshold[13]. Finally, lower biceps pre-activation in 0 *g*[14] cannot explain the observed timing shifts; supporting the forearm in 1 *g* with an external force reduced the tonic activation of the biceps without significantly changing EMG timing. Thus, the shifts observed during the flight were best explained by a failure to fully adjust for the lack of ball acceleration in 0 *g*.

Forearm movements were also affected by the lack of ball acceleration (**Fig. 2b**). In microgravity, these movements started much too early, but then stopped or reversed direction. The non-monotonic waveforms observed during the flight, but not on the ground, indicate that responses are not slower in 0 *g* because of reduced muscle tone[14]. Instead, once triggered, the CNS may modify the ongoing movement by updating estimates of TTC based on visual feedback[8,9,15]. Whereas forearm movements started prematurely for all tests during the flight, we found

Fig. 1. Test of TTC estimation during ball catching in 0 *g*. (**a**) Ball height versus time in 0 and 1 *g*. Dashed lines, expected impact time for a first-order TTC estimate applied in 1 *g* (red) and a second-order, 1 *g* internal model applied in 0 *g* (blue). White bars, fixed TTC threshold (λ) aligned with expected impact; colored bars, response lead (Δ) with respect to actual impact, for three different hypotheses. H_1, exact estimate of TTC based on real-time measurements of acceleration; responses are always triggered at the same time before impact ($\Delta_{1g} = \Delta_{0g} = \lambda$). H_2, first-order TTC estimate; the ball arrives earlier than expected in 1 *g* ($\Delta_{1g} < \lambda$). H_3, second-order internal model of gravity; the ball arrives later than expected in 0 *g* ($\Delta_{0g} > \lambda$). (**b**) Predicted time shifts (δ) for 0 *g* versus 1 *g* for different values of λ. H_1 predicts no difference ($\delta = 0$). Both H_2 and H_3 predict earlier responses with respect to impact in 0 *g* ($\delta > 0$); increasing λ increases δ. Shifts predicted by H_3 are greater for a given λ and rise more quickly as $v_0 \to 0$, compared to H_2.
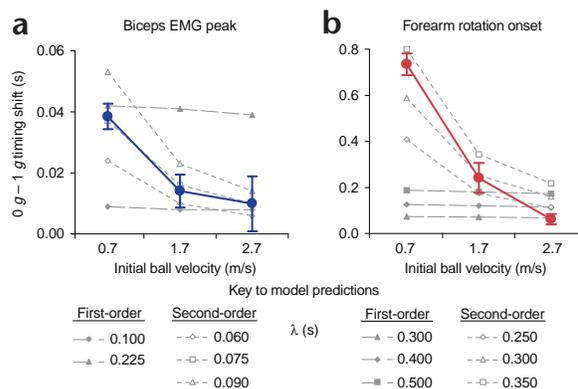
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Fig. 2. Anticipatory motor responses during catching in 0 and 1 *g*. Traces, average of 10 trials from a single subject and a single initial ball speed for (**a**) biceps EMG (v_0 = 0.7 m/s) and (**b**) forearm rotations (v_0 = 1.7 m/s).

Fig. 3. Timing of forearm rotations and biceps EMG compared to first- and second-order model predictions for different TTC thresholds (λ). Each data point represents the timing advance (δ) in 0 *g* for (**a**) biceps EMG peaks and (**b**) anticipatory forearm movements, averaged across subjects and sessions (± 1 s.e.m.).

evidence of adaptation to 0 *g* on flight days 9 and 15. The amplitude of the early, erroneous movement diminished and a later upward rotation developed just before impact.

The key experimental test (**Fig. 1b**) lies in the magnitude of time shifts for different initial ball velocities (v_0). The second-order, internal-model hypothesis predicts the non-linear increases in time shifts (δ) for decreasing values of v_0 using reasonable, fixed values of the TTC threshold (λ) (**Fig. 3**). These λ values are biologically plausible; a response initiated at λ = 75 ms within the brain is consistent with the arrival of the EMG peak in the muscle 40 ms before impact, due to neural transmission delays. Similarly, λ values of 300–400 ms are compatible with movement onset that normally occurs 200 ms before impact, given the time necessary to overcome limb inertia. In contrast, a first-order TTC estimate would require unreasonably long λ values ($\lambda \geq 1.2$ s, longer than the total drop time of the ball in 1 *g*) to reproduce the time shifts observed in 0 *g*. Furthermore, a first-order TTC estimate cannot, with a fixed λ, predict the substantial changes of initiation time as a function of v_0. Finally, had the subjects been able to directly measure the acceleration of the ball in real time, one would expect to see no time shift at all (with respect to impact) between 0 *g* and 1 *g*, irrespective of λ.

We conclude, therefore, that when catching a falling ball, the nervous system uses a second-order internal model of gravity to estimate TTC. On Earth, this makes sense, but why continue to use this model in 0 *g*? The astronauts could have adjusted more rapidly during the flight; they had visual cues indicative of the ball's constant velocity. Furthermore, the vestibular organs, pressure cues on the skin and visual cues from objects floating nearby clearly attest to the effective lack of gravity in orbit. On the other hand, the identifiable walls, floor and ceiling in the Spacelab, overhead lighting, and the

'upright' posture adopted most often by astronauts all confer a strong up–down sense to the working environment. Under these conditions, the brain gives credence to an internal model of the physical world in which a downward moving object should accelerate[3,4]. For the terrestrial conditions to which most of us are bound, the CNS improves its chances of success by using cognitive information about which way is 'down.'

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