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# **Research Reports**

# Load compensation in human goal-directed arm movements

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We analysed the execution of multijoint pointing movements in humans while weight or spring loads were applied to the pointing hand. Visual feedback on arm and hand position was excluded. Movement paths, final positions, and normalized velocity profiles were found to be load-independent, except for the very first movement after a load change. With increasing size of a weight load movement velocity decreased, and movement duration increased by the same factor, i.e. the velocity profiles were rescaled in magnitude and time. In contrast, under a spring load movement velocity and duration were not different from no-load controls. These findings led us to propose a new hypothesis on load compensation by the motor system. We suggest that an important controlled variable is a fictional force acting externally on the hand, and that the inertia- and gravity-related components of this force are controlled separately; then, loads are compensated by time scaling of the inertia-related, and magnitude scaling of the gravity-related component. The predictions of this hypothesis regarding movement paths and velocities under weight and spring loads are in good quantitative agreement with our experimental data. When specifically asked to do so, our subjects were able to generate velocity profiles under a weight load that were not different from those under no-load conditions, which suggests that alternative control strategies are available when needed.

## INTRODUCTION

We all can move a coffee-filled mug to our lips as proficiently as we can an empty Styrofoam cup, despite the different weights of the two objects. Our capability to do so is remarkable, since a change in weight requires quite complex changes in the pattern of muscle forces if the hand is to move along the same path. The intricate relationship between desired hand movement, imposed weight load, and required force pattern is formulated by the inverse kinematics and inverse dynamics equations in literature on robotics, where similar problems are encountered (see e.g. refs. 20,44).

The excellence of load compensation in humans has been confirmed by a group of quantitative studies that employed a variety of gravito-inertial, purely inertial, viscous or elastic loads<sup>3,13,14,28,38,43</sup>. These authors accordingly demonstrated that movement characteristics such as pointing accuracy, path travelled by the hand, shape of the hand tangential velocity profile, and coupling of shoulder and elbow motion, remain essentially unaffected by the applied loads.

In contrast, another group of studies revealed that motor performance *immediately after* an unexpected load change exhibited marked deviations from controls, persisting for several hundred ms<sup>5,12,24,39,40</sup>; similarly, deviations of

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comparable duration were found when subjects resisted unexpected loading or unloading of the hand<sup>22,34,45</sup>. The observed initial deviations have been attributed to the well-known transport delays of somatosensory-to-motor pathways, which range between 25 and 200 ms (overview e.g. in ref. 23).

In light of this evidence for sensorimotor delays in load compensation, it seems rather unlikely that the excellent performance documented by the above first group of studies is based on simple servocontrol principles. Rather, as discussed by some of the above authors, load compensation could be achieved by playing back previously established, generalized motor programs or motor tapes<sup>27,36</sup>.

This idea was elaborated quantitatively by Atkeson and Hollerbach<sup>3</sup>. Those authors observed that the tangential velocity profile of the hand, when normalized for movement amplitude and peak velocity, didn't change when a weight was carried in the hand. From this finding, they suggested the following hypothesis of load compensation. Assume that the variables primarily controlled by the brain are the torque profiles acting around the arm joints. Assume further that the torque profiles needed to move the arm along a desired trajectory are stored in the brain in two components, one to move the non-loaded arm, and the other to move a default external weight. Then, an r-fold weight is compensated when the magnitude axis of the weight-related torque profiles is scaled by r, while time axis and shape of those profiles need not to be altered; as well, no rescaling is needed for arm-related torque profiles.

To account for different movement speeds, Atkeson and Hollerbach<sup>3</sup> followed a suggestion by Hollerbach and Flash<sup>21</sup>: assuming that joint torques related to gravity can be separated from those related to inertia, a c-fold speed is achieved by scaling the magnitude of the inertia-related torques by  $c^2$ .

The outlined hypothesis is indeed compelling since it bypasses the laborious recalculation of inverse dynamics for each weight size and movement speed, replacing it by simple rescaling of prototype torque profiles. In particular, the pro-

posed principles for weight compensation and speed control are independent, in that scaling for weight doesn't change movement speed, and scaling for speed applies equally in the presence and absence of weight loads. Given the independence of weight and speed control postulated by the above hypothesis, we should expect that the presence or absence of a weight load doesn't affect the speed of an arm movement in a systematic way. This expectation is tested in the present study by analyzing original hand velocity profiles in addition to the normalized profiles investigated by Atkeson and Hollerbach<sup>3</sup>. Furthermore, a range of different weights rather than a single weight is used to support generalized conclusions on weight compensation. Finally, a spring load is used to determine if scaling principles apply to other load types as well.

#### MATERIALS AND METHODS

Six human subjects pointed with their right (preferred) hand at visual targets using the apparatus outlined in the inset of Fig. 1. The targets were presented through a mirror, and appeared to the subject at eye level 46 cm ahead against a totally dark background; lateral target position

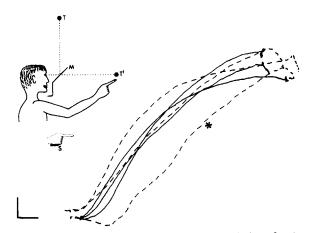


Fig. 1. Sample movement paths in the sagittal plane for the pointing index finger of one subject. Each line represents one movement; calibration marks are displacements of 50 mm forwards and upwards. Solid lines: no load; broken lines: 4.5 lb weight; asterisk: first movement with weight. The inset outlines the experimental setup. T: physical, T': virtual target position, M: mirror, S: support.

varied randomly within 9 cm off the mid-sagittal. The mirror and surrounding framework prevented vision of the pointing arm and hand.

The pointing movements were self-paced, starting with the hand on a support platform 34 cm below the mirror. Subjects indicated their readiness for a trial by pressing a button with the non-pointing hand; after a random delay of 1.0 to 2.2 s, a target appeared for 2.5 s. Subjects were instructed to point at the target as quickly and accurately as possible, to maintain the pointing position until the target disappeared, and to return the arm to the starting platform afterwards. Hand movement in the three dimensions of space was registered contact-free using an infrared lightemitting marker on the index fingertip, and the Watsmart motion analysis system (resolution better than 1 mm, frame rate 200 Hz). Since the movements were predominantly in a sagittal plane, only their forward and upward components were analyzed.

A lightweight clamp, attached to the subject's wrist, could be loaded with different weights. With the hand on the starting platform, the clamp rested on an additional support which prevented the subject from sensing the current weight magnitude prior to movement onset. The weights were changed between blocks of 5 movements, and thus could only be considered as unexpected for the first movement in a block. They were applied in the order 0, 1, 2, 2.5, 3.5, 4.5, 0, 4.5 pounds (lbs) for 3 subjects, and 0, 4.5, 3.5, 2.5, 2, 1, 0, 4.5 lbs for the other 3. For the final 4.5 lbs block, different instructions were provided: the subjects were asked to move at the same speed as in the just preceding 0 lb block, regardless of a possible reduction in pointing accuracy.

Since no differences were found between the responses in the first and second 0 lb block of each subject, nor between the responses with any given weight under the ascending versus the descending order of presentation, we concluded that order effects played a minor role for the kinematic variables under study, and pooled the data of all subjects.

In an additional experiment, blocks of trials with no load, a weight (2.5 lb), and a *spring* (35 N/m) were applied in a mixed order to the

same 6 subjects. The spring was attached to the subject's wrist on one end, and to a point 52 cm below the hand's starting platform on the other end. Spring stiffness and points of attachment were chosen to keep the spring just relaxed before movement onset, and to require extra muscle force during the movement that was roughly comparable in direction and magnitude to that needed for weight compensation (spring force at target position was 15.9 N, corresponding to a 3.6 lb weight).

#### **RESULTS**

## Movement paths

Fig. 1 illustrates that the movement paths of the pointing index finger in the sagittal plane exhibited a rather uniform, curvilinear shape that was not appreciably different when the hand was not loaded and when it carried a 4.5 lb weight. Only the very first movement after the load change followed a distinctly different path (asterisk in Fig. 1), deviating downwards near the starting position, and approaching the other paths again near the final position. Findings were similar for all weights under study and all subjects: movement paths didn't depend consistently on the external weight except for the very first movement in a block. That first movement exhibited a downward deviation after a weight increase and an upward deviation after a weight decrease, as one would expect for incomplete compensation. We concluded that the first movement in a block may represent a special category that should be studied separately, and focussed the present quantitative analysis on the remaining 4 movements in each block.

To find out whether final pointing position and pointing variability depended on the weight load, we calculated the mean final position and its S.D. for each subject and weight (incl. no load), and determined the intra-individual change of either measure between weight conditions. The calculated changes were not significantly different from zero (paired-samples t-tests: P > 5%), which indicates that mean pointing position as well as pointing variability were weight-independent. This analysis was applied with equal outcome to

the horizontal and to the vertical component of final pointing position, as well as to movement amplitude (defined as linear distance between initial and final position).

# Normalized velocity profiles

The velocity of the pointing finger in the upward and in the forward direction was analyzed separately. As we showed previously<sup>7</sup>, each component can be regarded as the sum of a smooth, single-peaked curve and a superposed 5 Hz oscillation, the latter probably due to 'noise' by intrinsic rhythmical activity in the motor system. In the present study, the oscillations were filtered out by 15-point central averaging of each profile (representing a low-pass filter with a -3 dB point of 3.7 Hz). The smoothed curves were then normalized for movement amplitude and speed in analogy to <sup>3</sup>, using

$$n(t) = \frac{P_0}{P} v \left( \frac{P_0 a}{P a_0} t \right) \tag{1}$$

where v and n are original and normalized velocity, respectively, a and p are amplitude and peak velocity, respectively, of a given movement,  $a_0$  and  $p_0$  are the average amplitude and peak velocity of movements executed by the same subject without weight, and t is time. Then, the normalized velocity profiles were aligned in time with respect to their peak values and averaged within each block.

The outcome of this evaluation is illustrated for one of our subjects in Fig. 2a,b. Clearly from these representations, the shape of upward and forward velocity profiles did not depend on the presence and size of a weight load. In an effort to quantify this observation, we calculated the skewness coefficient as ratio of acceleration time (from movement onset to peak velocity) and deceleration time (from peak velocity to the first approach of zero velocity). We felt that this ratio could be a particularly sensitive indicator of profile shape since acceleration and deceleration times are probably related to two different motor control processes<sup>29</sup> that may be affected differently by a load change. We found skewness to range around 0.75 and to be weight-independent (paired-samples t-tests of intraindividual skew-

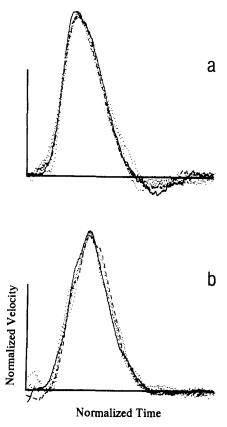
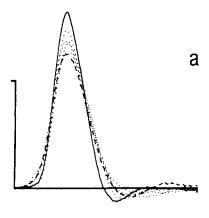


Fig. 2. a: upward, b: forward hand velocity profiles of one subject, normalized as indicated in the text. Solid lines: no load; broken lines: 4.5 lb weight; dotted lines: smaller weights. Axis lengths have no physical meaning due to normalization.

ness changes with weight: P > 5%), thus confirming the observations made in Fig. 2.

## Non-normalized velocity profiles

An additional characteristic of finger velocity profiles is disclosed by plotting them without prior normalization, as shown in Fig. 3 for the same movements as in Fig. 2. Clearly, these non-normalized profiles exhibit a conspicuous dependence on the applied weight, with peak velocity tending to decrease, and duration to increase, when the weight became larger; this effect appears similar in the upward and in the forward direction of movement. The findings didn't change appreciably when velocity profiles such as those in Fig. 3 were normalized for movement amplitude (but not for peak velocity), which is in keeping with the



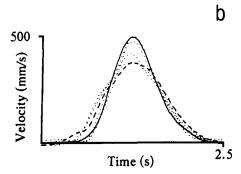


Fig. 3. a: upward, b: forward hand velocity profiles of the same movements as in Fig. 2, but without normalization.

Line types like Fig. 2.

above finding that movement amplitude is weight-independent.

We quantified the observed weight-dependence calculating the mean scaling  $(p_0a)/(p a_0)$  across all subjects for each weight applied. As shown in Fig. 4, the scaling factor increased consistently with increasing weight for both movement components, the weight dependence being slightly smaller in the upward direction. Linear regression analysis confirmed that the weight dependence was statistically significant: the mean correlation coefficient between weight size and scaling factor was 0.548 in the forward, and 0.585 in the upward direction, and was significantly different from zero for each subject (Fisher's t-test for correlation coefficients: P < 1% upwards, P < 0.1% forwards). Note that this is a conservative estimate since the relationship in Fig. 4 is not linear. Comparable results

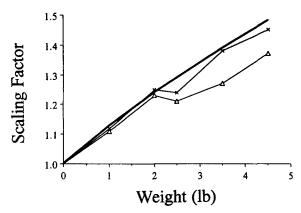


Fig. 4. Mean scaling factors for different weight loads, as calculated from experimental data on upward (triangles) and forward (crosses) hand velocity, and from the hypothesis outlined in Discussion and Appendix (bold line).

were yielded when scaling factors were calculated from movement duration rather than peak velocity.

Under each weight condition, the scaling factors exhibited some movement-to-movement variability. To find out whether forward and upward variability is correlated we determined, for each subject and weight, the *deviations* of the forward and upward scaling factors from their respective means. A subsequent linear regression analysis revealed that the forward and upward deviations were not significantly correlated (r = -0.346; Fisher's *t*-test for correlation coefficients: P > 5%, which indicates that the movement-to-movement variability of scaling factors is independent for the two directions.

Since the velocity profiles in Fig. 3 are shifted in time to align their respective maxima, information about the relative timing of the two components is not available from that representation. From further analysis, we found that the upward peak preceded the forward peak by 93 ms on the average, which was statistically different from zero (paired-samples t tests: P < 1%). This temporal order is in register with the curved shape of movement paths in Fig. 1.

# Experiments with a spring load

When the hand was loaded with a spring, shapes of the movement paths and normalized velocity profiles remained similar to those in Figs. 1 and 2, respectively. Also, paired-samples t-tests confirmed that skewness coefficient, final pointing position and pointing variability were not different from those obtained without a load. Most interestingly, non-normalized velocity profiles didn't exhibit a reduction of peak velocity and an increase of movement duration as they did under weight loads; this finding is illustrated for one subject in Fig. 5 (for this particular subject, forward velocity even slightly increased when the spring load was added). From data like those in Fig. 5, we calculated the mean scaling factor for our subjects as 0.95 in the upward, and 1.01 in the forward direction; neither value was significantly different from unity (1.00 was within the 99% confidence interval). We conclude that under a spring load the velocity profiles are not different from no-load controls, which is in clear contrast with the findings obtained under weight loads.

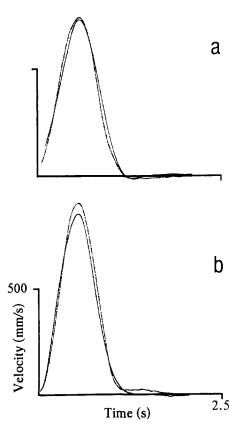


Fig. 5. Non-normalized hand velocity profiles of one subject in the a: upward, b: forward direction. Solid lines: no load; dash-dotted lines: spring load.

Experiments with prescribed timing

When the arm was loaded with a 4.5 lb weight and instructions required to move at the same speed as in the just preceding no-load condition, irrespective of a possible reduction in accuracy, we found that movement paths, normalized velocity profiles, final pointing position and pointing variability remained unaltered. However, non--normalized velocity profiles now differed clearly from those obtained with a 4.5 lb weight under the original instructions, and instead resembled closely the no-load profiles: the mean scaling factor was 1.03 in either movement direction. Thus, our subject succeeded in complying with the new instructions and speeded up the loaded movements to match the non-loaded ones. Moreover, they did so without deterioration of pointing accuracy.

## DISCUSSION

The present experiments demonstrated that the compensation for external loads in goal-directed arm movements is remarkably fast and efficient. Already the second movement after a load change did not differ with respect to final accuracy, movement path, and normalized velocity profile from movements executed before that change. This finding is in line with the two groups of studies referred to in the Introduction, one revealing altered movement characteristics immediately after an unexpected load change (like our first movement in a block), and the other well-compensated motor performance (like our second to fourth movements in a block). We therefore conclude that our data confirm both groups of studies, and additionally suggest that a single movement may be sufficient to achieve compensation.

Since we excluded visual feedback on the pointing arm, the only remaining source of information on current load size and on load-induced changes of the hand movement path were tactile-proprioceptive afferents from the arm. It therefore appears from our data that afferent signals are sufficient for an adequate load compensation. This outcome is related to previous studies, comparing the accuracy of passive and active arm

movements without visual feedback: the reasonable performance under passive conditions suggested that afferents may well contribute to motor control<sup>10,32</sup>, although the improved active performance underlined the role of efferent mechanisms.

Our finding, that the movement-to-movement variability of forward and of upward velocity is not correlated, indicates that biological noise is generated predominantly in those parts of the motor system that are laid out in parallel for these two directions. If we assume that mechanisms generating most noise are also most heavily involved in the control process<sup>6</sup>, we can conclude that motor control has a predominantly parallel, direction-specific organization. Such a conclusion is in accordance with available neurophysiological data on the direction-specific organization of motor control<sup>9,25</sup>.

The most salient finding of the present study is the consistent dependence of movement speed and duration on the size of an applied weight: non-normalized velocity profiles were compressed in magnitude, and expanded in time by the same factor, when the weight became larger. This result is in principal agreement with previous findings on lower movement velocity with larger weight loads<sup>14,17,28,35</sup>. It also can be reconciled with the load compensation hypothesis by Atkeson and Hollerbach<sup>3</sup> outlined in the Introduction: although according to that hypothesis weight and speed are controlled separately, a coupling between the two is principally possible. It should be noted, however, that the hypothesis doesn't readily explain why such coupling should occur, nor what size of speed change to expect with a particular weight.

In light of the above shortcomings, we propose a new, substantially different hypothesis that readily predicts our experimental findings. The new hypothesis is based on the following two assumptions, which differ from those by Atkeson and Hollerbach<sup>3</sup>: firstly, the variable primarily controlled by the motor system is a fictional force acting directly on the subject's hand, similar to the forces controlling the limbs of a marionette; lower-level

motor centers can transform that fictional force into a set of muscle contraction commands\*. Secondly, the fictional force can be subdivided into two separately controlled components, one related to gravity and the other to inertia. Note that our second assumption is similar to the third assumption by Atkeson and Hollerbach<sup>3</sup>, allowing to control movement speed in the same way. Note also that we do not separate the control of arm and load movement, which reduced the total number of assumptions by one. We consider first the compensation of the inertial component of a weight load. As determined in the Appendix (Eqn. A14), a load mass  $m_L$  is compensated when the fictional force profile is scaled in time with factor

$$k = \sqrt{\frac{m_{\rm A} + m_{\rm L}}{m_{\rm A}}} \tag{2}$$

where  $m_A$  is the apparent mass of the subject's arm and k > 1 denotes increased time. Further from the Appendix (Eqn. A15), this time scaling of force yields hand velocity profiles that are scaled in magnitude by 1/k and in duration by k, obviously in qualitative agreement with our experimental findings. For a quantitative comparison we set  $m_A = 1.7 \, \text{kg}$  as determined in the Appendix, calculated k for the  $m_L$  applied using Eqn. 2, and plotted the outcome along with the experimental data in Fig. 4. The good agreement between theoretical and experimental results in that figure clearly supports the validity of the new hypothesis.

Further support comes from experimental data kindly provided to the author by Dr. J.B.J. Smeets from the Rijksuniversiteit in Utrecht, the Netherlands. These data, collected with a different apparatus and for a different purpose, include the peak hand velocity of two subjects under a 5.0 kg and a 0.7 kg load. Since arm configuration around peak velocity was comparable to that in our study except for a different orientation to gravity, we assume  $m_L \approx 1.7$  kg for the Utrecht subjects as well. Then from Eqn. 2, k = 1.19 and 1.99 for the two loads, and consequently the

<sup>\*</sup> This can be done by geometrical projection operations, e.g. by applying the transpose Jacobian matrix.

respective peak velocities should be related by 1.99/1.19 = 1.67. This prediction of our hypothesis compares well with the experimental ratio of 1.73. We conclude that the proposed time scaling of force profiles may be effective for weights up to at least 5 kg.

Obviously, the fictional force related to gravity must be scaled in time by k as well to maintain synchrony with the inertia-related force. However, such a scaling will not compensate for the gravitational effects of the weight; therefore, an additional mechanism must be considered for gravity compensation. Following the arguments of Atkeson and Hollerbach<sup>3</sup>, this mechanism may be magnitude scaling of the gravity-related force by  $k^2$ .

The proposed distinction between scaling principles for inertia and those for gravity is supported by the outcome of our experiments with spring loads. Since the spring added little inertia to the arm, it can be likened to a gravitational load that gradually increased in size and changed in direction throughout the movement. According to the above considerations, such a load should be compensated by magnitude scaling which doesn't affect movement velocity and duration. Indeed, this prediction is met by our experimental data: the scaling factor of spring-loaded movements remained close to unity.

The proposed distinction between inertia and gravity seems advantageous for other purposes besides load compensation. It allows the control of movement speed by simple scaling principles<sup>21</sup>, and it simplifies movement control under changing body positions: an arm movement that remains unchanged in a body-centered frame, but is performed e.g. once while seated and once while lying, requires no changes of the inertiarelated force, and only a *rotation* of the gravity-related force. Recent single-cell recordings documented that the motor control system is indeed capable of fast rotational transformations<sup>16</sup>.

The first assumption of the new hypothesis, that the controlled variable is a fictional force acting on the hand, implies that forces are planned by the motor system in task space rather than in joint space. Similarly, previous work suggested that movement *paths* are planned at task-level<sup>1,15</sup>.

We therefore conclude that our hypothesis extends the scope of task-level planning beyond movement kinematics to include movement dynamics as well. The present assumption is also appealing introspectively: when we lift a heavy object, we intend to generate a force by the hand rather than to contract muscles or to rotate joints. The concept of a fictional force is reminiscent of the previously proposed 'desire vector'18 and 'force disturbance vector'31, imaginary external forces that would move the hand along a desired trajectory given some presumed mechanical properties of the arm. Those vectors were introduced to solve the inverse kinematics of the arm, and were not applied to problems of dynamics such as load compensation.

Clearly, systems as complex and versatile as the human motor control system are unlikely to abide to a single set of rules. Rather, we expect that different strategies will be employed depending on the constraints of a particular motor task. Indeed, our subjects demonstrated such a flexibility. When specifically instructed to do so, they were able to compensate for a weight without changing arm velocity. In related studies, subjects could keep movement time constant while the inertial load was varied<sup>4,38</sup>, or varied movement time while the load remained unchanged<sup>46,4,37</sup>.

#### APPENDIX

Movement of the arm under a fictional force acting on the hand

When a force F(t) acts on point H of an articulated body, the acceleration A(t) of H is given by

$$A(t) = \frac{1}{m_{\Delta}} F(t) \tag{A1}$$

where A and F are spatial vectors, t is time, and  $m_A$  is a coefficient we will call 'apparent mass' of the body: replacing the body by a point mass of size  $m_A$  in H would not change the magnitude of A(t) in response to the same F(t). Note that in articulated bodies:

- the size of  $m_A$  depends on the body's momentary configuration;

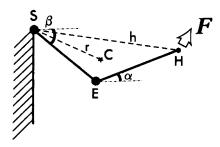


Fig. A1. Simplified human arm. S: shoulder, E: elbow, H: hand, C: center of mass,  $\alpha$ : elbow angle,  $\beta$ : shoulder angle; F: force acting on H. S and E are hinge joints with axes perpendicular to the drawing plane; angles are measured with respect to the horizontal.

- the size of  $m_A$  depends on the direction of F;
- the directions of F and A may differ\*\*.

The concept of apparent mass is closely related to that of apparent stiffness<sup>31</sup>, only we propose that inertia rather than elasticity dominates arm mechanics which allows a straightforward interpretation of our experimental findings.

To determine the apparent mass of the arm under F(t), we simplify the arm as shown in Fig. A1, and calculate the movement of that arm under a unit external force  $F_{\varepsilon} = 1$  acting on H at a given instant of time in direction  $\varepsilon$ . As a second simplification, we will neglect the contribution of joint-interaction terms to the arm movement (see ref. 21). One component of  $F_{\varepsilon}$  moves H around E with acceleration  $a_{\gamma}$  in direction  $\gamma$  where

$$a_{\gamma} = \frac{\sin\left(\varepsilon - \alpha\right)}{m_2/2} \tag{A2}$$

$$\gamma = 90 + \alpha \tag{A3}$$

with  $m_2$  the forearm mass. The other, orthogonal component of  $F_{\varepsilon}$  is transmitted across E to S and partly absorbed there; the remaining part moves H around S with

$$a_{\delta} = \frac{\cos(\varepsilon - \alpha)\sin(\alpha - \beta)}{r/h(m_1 + m_2)}$$
 (A4)

$$\delta = 90 + \beta \tag{A5}$$

where  $m_1$  is the upper-arm mass, h the distance between H and S, and r the distance between the arm's center of mass and S (see Fig. A1). r/h can be interpreted as the leverage in H around S, and calculated from elementary physical considerations as

$$r/h = \sqrt{\frac{(m_1 l_1/2 + m_2 l_1)^2 + (m_1 l_1/2 + m_2 l_1) m_2 l_2 \cos(\alpha - \beta) + (m_2 l_2/2)^2}{((l_1)^2 + 2 l_1 l_2 \cos(\alpha - \beta) + (l_2)^2) (m_1 + m_2)^2}} \quad \left(A6\right)$$

Total acceleration  $a_{\varepsilon^*}$  under  $F_{\varepsilon}$  is the vector sum of  $a_{\gamma}$  and  $a_{\delta}$ , with

$$a_{\varepsilon^*} = \sqrt{(a_{\gamma})^2 + (a_{\delta})^2 + 2a_{\gamma}a_{\delta}\cos(\delta - \gamma)}$$
 (A7)

$$\varepsilon^* = \operatorname{atn} \frac{a_{\gamma} \sin \gamma + a_{\delta} \sin \delta}{a_{\gamma} \cos \gamma + a_{\delta} \cos \delta}$$
 (A8)

Note again that in general  $\varepsilon^* \neq \varepsilon$ . Finally, since from Eqn. (A1)  $m_A$  is the reciprocal acceleration in response to a unit force, we have

$$m_{\rm A} = \frac{1}{a_{\rm c^*}} \tag{A9}$$

Estimating  $m_A$  in our subjects

For further calculations, we need to know the size of  $m_A$  at the times of peak forward and upward velocity, i.e. those instants used for the scaling factors in Fig. 4. We therefore measured in our subjects  $l_1$ ,  $l_2$ ,  $m_1$ , and  $m_2$ , the latter two by volumetry and assuming with ref. 2a specific weight of 1.035. Furthermore, we determined from our recordings the finger positions at peak forward and upward velocities, replicated the subjects' arm postures at those instants, and measured the respective values of  $\alpha$  and  $\beta$ . (One subject was no longer available; for him,  $\alpha$  and  $\beta$ were estimated from his other anatomical data). Finally, since peak upward velocity preceded peak forward velocity, we can set  $\varepsilon^* = 90^{\circ}$ during the former, and  $\varepsilon^* = -90^{\circ}$  during the latter peak.

Using the above values, we calculated  $\gamma$ ,  $\delta$ , and r/h from Eqns. A3, A5, A6, then  $a_{\gamma}$  and  $a_{\delta}$  from Eqns. A8, A2, A4, and finally  $m_{A}$  from Eqns. A7, A9. The results (mean  $\pm$  S.D.) thus yielded were

<sup>\*\*</sup> The latter two properties can be expressed more compactly by replacing the scalar  $m_A$  in Eqn. A1 with the body's inertia matrix. In the present manuscript, however, the scalar notation will be maintained for better transparency of the calculations.

 $m_{\rm A}=1.41\pm0.31\,{\rm kg}$  for the forward, and  $m_{\rm A}=1.97\pm0.56\,{\rm kg}$  for the upward velocity peak, the difference between both being marginally significant (paired-samples *t*-test on intraindividual differences: P<5%). For further calculations, the average  $m_{\rm A}=1.7\,{\rm kg}$  was used. In passing,  $\varepsilon$  at both instants was quite close to  $\varepsilon^*$ ; their absolute difference averaged 23.5 deg.

To determine the sensitivity of  $m_A$  to small inaccuracies in the values we used for the above calculations, we re-calculated  $m_A$  after increasing or decreasing either value by 10%. The resultant changes of  $m_A$  were always smaller than 10%, which suggests that our estimate of  $m_A$  is rather robust.

# Compensation for inertial loads

With a load mass  $m_{\rm L}$  added to the hand, the new apparent mass becomes  $m_{\rm A}+m_{\rm L}$ , and Eqn. A1 changes to

$$A(t) = \frac{1}{m_{\rm A} + m_{\rm I}} F(t) \tag{A10}$$

with  $\varepsilon^*$  matching  $\varepsilon$  even closer than without a load. When the load is compensated by time scaling of F, the new hand velocity V' and position P' are related to original velocity V and position P by

$$V'(t) = \frac{k}{m_{\Lambda} + m_{L}} \int F\left(\frac{1}{t}\right) d\left(\frac{1}{t}\right) = \frac{km_{\Lambda}}{m_{\Lambda} + m_{L}} V\left(\frac{1}{t}\right)$$
(A11)

$$P'(t) = \frac{k^2}{m_A + m_L} \iint F\left(\frac{1}{k}t\right) d\left(\frac{1}{k}t\right)^2 = \frac{k^2 m_A}{m_A + m_L} P\left(\frac{1}{k}t\right) \quad \text{(A12)}$$

where k is the scaling factor (duration increases for k > 1). We know from our experimental data that the hand movement path doesn't change with a weight load, i.e.

$$\mathbf{P}'(t) = \mathbf{P}\left(\frac{1}{k}t\right) \tag{A13}$$

and consequently from Eqn. A12

$$k = \sqrt{\frac{m_{\rm A} + m_{\rm L}}{m_{\rm A}}} \tag{A14}$$

We finally have from Eqns. A11, A14

$$V'(t) = \frac{1}{k} V \left(\frac{1}{k}t\right) \tag{A15}$$

i.e. the new velocity profile is scaled in magnitude by 1/k, and in time by k.

It should be noted that k is not a constant: since  $m_A$  varies throughout the movement, so does k (see Eqn. A14). In the present work, we only considered the value of k attained around peak hand velocity, i.e. for  $m_A \approx 1.7$  kg, since this is when the scaling factors have been determined from our experimental data.

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