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A model of motor performance during surface penetration: From physics to voluntary control

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Abstract

The act of puncturing a surface with a hand-held tool is a ubiquitous but complex motor behavior that requires precise force control to avoid potentially severe consequences. We present a detailed model of puncture over a time-course of approximately 1000 ms, which is fit to kinematic data from individual punctures, obtained via a simulation with high-fidelity force feedback. The model describes puncture as proceeding from purely physically determined interactions between the surface and tool, through decline of force due to biomechanical viscosity, to cortically mediated voluntary control. When fit to the data, it yields parameters for the inertial mass of the tool/person coupling, time-characteristic of force decline, onset of active braking, stopping time and distance, and late oscillatory behavior, all of which the analysis relates to physical variables manipulated in the simulation. While the present data characterize distinct phases of motor performance in a group of healthy young adults, the approach could potentially be extended to quantify the performance of individuals from other populations, e.g., with sensory-motor impairments. Applications to surgical force-control devices are also considered.

Keywords

haptic; motor; model; force control; physics; biomechanics; oscillation; application

The act of puncturing a surface with a hand-held tool occurs ubiquitously in human behavior, in actions from mundane (spearing food with a fork) to highly skilled (surgery). This action is not only commonplace, but also intrinsically complex. The goal is generally not only to penetrate, but also to control forces after penetration, in order to minimize subsequent distance traveled and/or prevent damage to the substrate. Contributing to the complexity of puncture is the time-varying nature of factors that govern forces on and exerted by the actor, which transition from the purely physical interaction between effector and surface at the point of penetration, through passive biomechanical mechanisms, to voluntary activation of muscles. Modeling these factors and their time-course could have considerable value, not only for our basic understanding of motor behavior but also in application, as discussed below.

With these goals in mind, we used kinematic measurements from a high-fidelity force-feedback device to model the initiation and response to puncture. Using a pen-shaped handle, young adult subjects pushed or pulled on a simulated membrane, under instructions to penetrate while minimizing further distance beyond its boundary. The simulation was intended to capture essential physical characteristics of resistance and damping that would modulate motor behavior (see Prattichizzo et al., 2012, for a similar approach). Kinematic data up to approximately 1 s after puncture were used to develop a three-phase model of motor behavior. Phase 1, just after the burst through the membrane, is governed purely by

physics: The point of burst corresponds to the release of a resisting force F . The classical $F=ma$ relation then dictates an instantaneous acceleration a_0 , resulting from the breakthrough force in combination with the mass of the hand/ device coupling. Phase 2 occurs as biomechanical factors come into play. Models of muscle and tendon relaxation (e.g., Fung, 1967; Sarver et al., 2003) indicate that once stress is reduced, force declines due to the highly viscous nature of the musculo-tendon system, quickly taking an exponential form (Milner-Brown, 1973; Kisiel-Sajewica et al., 2005). Extrapolating from these models to the puncture task, which involves complex, multi-joint control, is of course not possible. However, exponential decline after release has the advantage of being a simple and general model for viscous behavior, and we accordingly chose this form to model the post-burst force/time relation¹. In Phase 3, deviations from the model are detected. These are attributed to the onset of active braking, which is subject to residual physical and biomechanical factors as well as voluntary control processes. In spatially directed (cf. force controlled) actions, active control has been modeled as a series of iterative corrections (e.g., Meyer et al., 1988), which can lead to oscillations around the target endpoint (Milanovic et al, 2000; although oscillations have also been attributed to emergent consequences of the neuromuscular system, see Feldman & Levin, 2009).

As applied to kinematic data from individual trials, our model allows us to estimate three key parameters: the mass coupling of the person to the device controller (including its inherent mass), the time constant of exponential force decay, and the onset of active braking, as indicated by deviation from the exponential model. From the fit data, specific predictions were tested, particularly pertaining to the effects of membrane stiffness: (i) People will exhibit essentially constant mass coupling of the person to the device, with the result that acceleration at the point of burst will have a direct linear relation to the stiffness of the simulated membrane (which governs the burst force). (ii) Following the physical breakthrough of the membrane, initial displacement and velocity should be described by an exponential decline in force. It is expected, given biomechanical constraints, that the time-course of this exponential will narrow with the initial velocity (Jaric et al., 1997), which in turn directly depends on stiffness. (iii) The time of active braking onset, as indicated by deviation from the exponential force-decay model, will depend on the strength of the sensory signal indicating puncture, which in turn will increase with stiffness. More specifically, behavioral measures of reaction time and estimates of cortically mediated sensory-motor loops suggest that, given a robust sensory signal, active braking onset will have a lower bound on the order of 100 ms and an upper bound on the order of 200 ms. (Johansson & Flanagan, 2009; Lipps, 2011; Woodworth & Schlossberg, 1960; Weiss & Flanders, 2011). Near-threshold signals, which might occur with low-stiffness membranes, could lead to substantially slower reactions. (iv) The general form of the kinematic trajectory and its variability across model parameters and individuals is not predicted per se, but can be characterized from the data. A question is whether the effects of stiffness, which are assumed to dominate early post-puncture behavior, can still be seen over the course of active braking.

¹Note that our model does not assume an underlying mass-spring system, as it applies to active braking in response to a sudden release of resisting force while moving. Fitting a mass/spring model in our task would require an additional parameter beyond the biomechanical stiffness, namely, the zero point of the system. Instead we begin with the impulse force from membrane puncture and describe its passive decline as exponential. We also evaluated linear force decay, which was obviously inferior in fit to the data over its entire time-course.

Method

Subjects

The subjects were 8 adults, 4 male and 4 female, affiliated with the local university community. All gave informed consent, consistent with institutional approval.

Apparatus

A virtual membrane was simulated on a 6-DOF magnetic levitation haptic device (MLHD) from Butterfly Haptics (Maglev 200TM, see <http://butterflyhaptics.com>). The MLHD uses Lorentz forces for actuation, which arise from the electromagnetic interaction between current-carrying coils and magnets (Hollis & Salcudean, 1993). Since there are no motors, gears, bearings, or linkages present, it is free of friction and capable of rendering forces and virtual springs with high fidelity, with an updating rate up to 4 kHz for force feedback and a positioning bandwidth of 140 Hz. The spatial resolution of the device is 2 μm and 3.6 arc-sec, respectively, for translational and rotational motion. In the present study, it was connected to a client PC through a 100 Mbps Ethernet cable. A multi-threaded application was run to command the MLHD to create the virtual membranes and record the subjects' interaction with them. To interact with the device, the subject grasped a cylindrical acrylic handle 14.34 cm long and 0.94 cm in diameter, weighing 11.8 g, which was held like a pen.

All stimuli were presented through haptic feedback alone; the visual context was uninformative. The inner edge of the virtual membrane was haptically rendered as a circular surface that enclosed the resting position of the maglev handle's attachment point. To prevent subjects from anticipating the precise membrane position, the length of the radius from attachment to the simulated membrane edge was drawn for each trial from a uniform distribution over 0.5 to 1.5 mm. Subjects were instructed to move the MLHD handle either in a forward downward direction (push) or backward upward direction (pull); movement in the directed quadrant of the membrane-defined plane, which was essentially frontal to the subject, was enforced by the device. The mass of the flotor was approximately 500 g. Its weight was cancelled by an upward force, and viscosity (15.0 N*s/m) was applied to enhance stability. At the prescribed distance from resting position, the membrane was implemented as a Kelvin-Voigt model with viscosity of 20.0 N*s/m and one of 4 spring constants that varied over trials: 600 N/m, 1130 N/m, 1660 N/m, and 2200 N/m.² Penetration of the near membrane boundary caused the spring/damper model to be enacted for a further distance of 0.5 mm. Full passage of that distance, constituting the virtual membrane's width, yielded spring-determined forces of 0.30 N, 0.56 N, 0.83 N and 1.10 N; a relatively small additional velocity-dependent force was produced by the viscosity (see below). Upon crossing the far membrane boundary, puncture was simulated by releasing the spring force and returning to the weightless status with only a viscosity of 15.0 N*s/m. The haptic rendering was updated at a rate of 1 kHz.

Procedure

The experimental variables were direction of movement toward the membrane (push or pull) and the spring constant (4 values). Each combination was implemented 10 times in random order, with 10 practice trials preceding the experiment without feedback. Each trial began with the direction of movement appearing on-screen. The subject then freely moved the handle until the membrane was encountered and punctured. The instructions specified that

²These values are not equally spaced because of sensitivity constraints on the low end and stability constraints on the high end. Preliminary testing with a lower value, though above the force threshold previously found for this device with a similar manipulandum and normal forces (approximately $.16 \pm .04$ N), showed that subjects often did not detect the membrane. Although the lowest value used here is well above threshold, the data suggest that subjects still failed to detect the weakest membrane on some trials.

thereafter, the distance traveled in the same direction was to be minimized. Whether or not the subject had fully stopped, the trial ended after 2 s spent continuously beyond the far boundary, at which point the handle was released and automatically re-centered.

Modeling penetration behavior

Position data in the plane of approach (relative to the point of attachment of the handle) were acquired by the MLHD at 200 Hz and were analyzed for each trial to separate stages of motor behavior as described above. In Phase 1, breakthrough, the initial force exerted by the hand on the flotor is expressed by:

$$F_0 = K * D + \delta * \gamma * v_0 \quad (1)$$

where K, D, and γ are rendering-specified parameters: K is the spring constant, D is the distance traveled in contact with the membrane, and γ is the additional viscosity within the membrane relative to the post-breakthrough environment. The parameter v_0 is the velocity at breakthrough, which was estimated by the slope of a linear function fit to the final pre-breakthrough positions within the membrane (see analysis section). Given these known parameters, a cubic function was fit to the first 9 distance observations (45 ms) after the membrane boundary (**a value which generally gave a good cubic fit**), and the derivative was solved for the precise breakthrough time t_0 , which generally fell between data points. The double derivative of the same cubic fit to distance was then used to estimate the initial acceleration a_0 , and from the known F_0 , to estimate inertial mass, m.

In Phase 2, force at breakthrough declines in the form of an exponential decay, with an additional damping component from the viscous environment. This is expressed by the following equation:

$$F(t) = F_0 * \exp(-t/\tau) - \gamma * v \quad (2)$$

where F is the applied force, t is the time relative to breakthrough, F_0 is the force at breakthrough (that is suddenly no longer countered) from Equation (1), τ is the time constant for the exponential, and $\gamma * v$ is the further damping imposed by the viscosity (γ), and the current velocity (v). Figure 1 shows predicted distance and velocity over time subsequent to puncture during Phase 1 and 2, for combinations of levels of two critical parameters, the stiffness K, which is dictated by the rendering, and the exponential time constant τ . In the velocity function, the effect of K is clearly evident in the initial slope, while τ governs the later rate of decline.

The model is fit to the data in order to estimate the time constant of the exponential, τ . Beginning with the previously derived estimates of mass, burst force, and acceleration at t_0 , the model predicts the position of the needle tip from the membrane over time-steps of 0.5 ms. At each time-step it starts with current force, computes acceleration as F/m , then computes current velocity and finally position. The value of τ was determined by selecting an observed time-point (at approximately twice the time to peak velocity), then running the model iteratively to find the τ that minimized the difference between predicted and actual distance from the membrane at that point. Tests with varying starting points showed that this method generally led to consistent estimates over a region beyond peak velocity and before active braking would be expected, which is the region in which force decline governed by the **parameter is expected**.

The assumption of exponential decline in force, which predicts a smooth decline of velocity to zero, is not expected to describe the data for the full time-course after breakthrough. Subjects will eventually initiate active braking, constituting Phase 3 of the model. Its onset

was calculated by finding a time-point where the model and data deviated. This braking point was identified by smoothing the velocity data with local polynomial regression, then working backward from the first zero crossing of velocity to the first data-point where the sign of the difference between predicted and observed values reversed. For a further 500 ms beyond the braking point, oscillations (changes in direction) were identified (see analysis section) and descriptive parameters were computed. This interval was selected because of variable numbers of observations beyond that point and the fact that 1/2 sec is sufficient time for a controlled hand movement (e.g., Jeannerod, 1984).

Results

The process described above yields parameter estimates for each individual trial. Along with relevant kinematic data, these were subjected to statistical analysis. Unless otherwise indicated, **repeated-measures** analyses of variance (ANOVAs) were conducted, based on the individual-subject means over trials for each combination of the experimental factors: direction of movement (push vs. pull) and membrane stiffness (K: 4 values). Alpha was set to .05. Criteria for exclusion of a small subset of trials are described below.

Velocity in membrane at puncture

Working backward from the outer edge of the membrane, a linear function was fit to the final values of position, the slope of which estimates the velocity at burst, the model parameter v_0 . Trials that could not be fit with linear $r^2 \geq .85$ or greater, over at least 3 and up to 10 successive pre-penetration position measurements, were discarded. These constituted 22 trials (3%), almost all with low stiffness, where sensing when the membrane had been entered was evidently not reliable. As would be expected from movement against resistance, the values of v_0 for the 618 trials with good linear fits declined monotonically with stiffness (mean 0.20, 0.13, 0.12, and 0.10 cm/s for $K = 600, 1130, 1660$, and 2200 N/m), $F(3,21) = 12.33$, $p < .001$. These correspond to average forces at puncture, due to stiffness and viscosity within the membrane, of 0.31, 0.57, 0.84, and 1.10 N. There was essentially no effect of movement direction or interaction, both $F_s < 1.0$.

Modeling post-burst behavior

Trials were fit individually to the exponential-force-decay model, by the process described previously. At this point in the analysis, 25 additional trials were eliminated, because of slow stopping (the first velocity zero-crossing occurred later than 550 ms: 19 trials) or other erratic behavior that precluded model fitting (6 trials). For the 593 remaining trials, considering data points from the empirically extracted t_0 to the point where deviation from the model was detected, the r^2 between predicted and observed distance values, **as computed for individual trials**, averaged over 0.99 across trials. **Only two trials retained in the analysis had r^2 values less than .90.** Figure 2 shows fits to distance and velocity for two trials over 500 ms following burst through the membrane. From the fits to the model the following parameters were extracted for each trial: time to the first zero crossing of velocity and distance at that time, inertial mass, time constant, and braking time (point of deviation from the model).

Stopping behavior

Stopping efficacy was indicated by the time to reach the first zero crossing of velocity and the distance from the membrane reached at that time-point, termed “skid.” These measures are shown in Figure 3. Effects of stiffness were found in the ANOVA on time to zero velocity, $F(3, 21) = 45.26$, $p < .001$, and distance to zero velocity, $F(3, 21) = 14.44$, $p < .001$. Subjects’ velocity declined faster with higher stiffness, but not enough to prevent going further before it reached zero. Effects of movement direction were also found for both time

to zero velocity, $F(1,7) = 11.83$, $p = .011$, and distance, $F(1,7) = 11.33$, $p = .012$. Movement in the pull direction showed an advantage both in a faster decline of velocity and a shorter distance traveled at the zero crossing. No interaction was obtained in either the time or distance ANOVA.

Mass

The assumption of constant inertial mass predicts a linear relation between initial acceleration and the force at burst, which is controlled by the membrane simulation. Figure 4 shows a strong linear fit for both directions of movement. Estimates of mass from the inverse slope were 522 g for the pull direction and 507 g for push. These values are very nearly the intrinsic mass of the flotor (approximately 500 g), indicating that the coupling of subjects to the device added relatively little mass to the system. The ANOVA on mean mass estimate over individual trials found no reliable effects for stiffness or direction of movement, confirming that the experimental manipulations had little effect on subjects' interaction with the device. Masses estimated for individual subjects from averaged trial data ranged from 498 g to 539 g, with a s.d. of 17 g. The within-subject s.d. averaged 81 g for pull and 83 g for push, about 16% of the intrinsic mass estimate (500 g).

The time-course of exponential force decline in Phase 2, as measured by the model parameter τ , tended to decrease with membrane stiffness, as shown in Figure 5. This trend echoes the previously noted faster zero-crossing of velocity when the membrane was stiffer. **The within-subject s.d. in τ** averaged .06 s for pull and .07 s for push; within-subject s.d. was less than the between-subject s.d. for all combinations of stiffness and movement direction.

Similarly to the trend with τ , the deviation point of the data from the model, which provides an indication of the onset of active control of braking (Phase 3), tended to be earlier with higher values of stiffness. This can be attributed to earlier detection of puncture with a larger force-change signal. To assess whether the dependency of deviation time and τ on experimental manipulations was similar, a $2 \times 2 \times 4$ ANOVA treated these measures as levels of a single factor, time-measure, along with the experimental factors of movement direction and stiffness. The dependent variable was the measured time, either τ or deviation as appropriate.

There were significant effects of time-measure, $F(1,7) = 46.60$, reflecting the temporal lag between τ and deviation. This lag, which averaged 199 ms, was fairly consistent across the experimental manipulations, as indicated by the failure of interactions involving time-measure to reach significance. The effect of stiffness was also significant, $F(3, 21) = 34.08$, $p < .001$, reflecting the tendency for a faster force decline for larger K. The main effect of direction was significant, $F(1,7) = 19.50$, $p = .003$, due to the tendency for the time-course of force decline to be earlier for pulling than pushing.

Active braking

Participants rarely came to a smooth stop, but rather reversed the forward movement one or more times, as shown in Figure 6. Ultimately, their stopping point tended to be closer to the membrane boundary than would be predicted by an exponential decline of force. As estimated 500 ms after the deviation point, the actual stopping distance was 12% below the model-predicted distance for the lowest stiffness value and 23% below predicted across the three higher values, where it did not reliably differ, $t(7) = 2.95$, $p < .05$. The percentage reduction in stopping distance was statistically constant across movement direction.

Oscillations during braking were detected from position observations (i.e., distance from the membrane outer edge) over 500 ms from the braking onset, after smoothing with an 11-point average. Each oscillation was defined by three successive reversals of direction. Its amplitude was measured by the absolute difference between the position at the middle reversal and the mean position at the preceding and following reversals; its duration was the time between the first and third reversal. The end of one oscillation was the first point in the next, and so on. Of the 593 trials, 71% had at least one detectable oscillation, 32% had at least two, and 13% had three or more. The number of oscillations in a single trial varied from 0 to 7 with an average of 1.27, and there was no systematic tendency for this behavior to vary with stiffness or movement direction.

To assess differences in successive oscillations and the effects of experimental variables, we conducted an ANOVA using data from the 192 two-oscillation trials only ($N = 44, 51, 45$, and 52 over the four stiffness levels). This analysis, with factors oscillation number (first, second), stiffness and movement direction, used individual trials as the unit of analysis, because while all subjects produced at least one trial with two oscillations, they are not all represented in each cell of the factorial design. The peak amplitude of the first and second oscillation averaged 0.12 mm and 0.03 mm, and the durations were 182 ms and 122 ms, respectively. The drop in peak amplitude from the first to the second oscillation was significant, $F(1, 184) = 110.30$, $p < .001$, as was the drop in duration, $F(1, 184) = 40.44$, $p < .001$. The oscillations were not independent. There was a positive correlation between the first and second oscillation's amplitude, $r = 0.22$, $p = 0.003$, and a significant negative correlation between durations, $r = -0.34$, $p < 0.001$. Thus more intense first oscillations persisted to second oscillations, but a longer first oscillation shortened the second.

Stiffness affected the intensity of both oscillations. Peak amplitude showed both a main effect of stiffness, $F(3, 184) = 14.74$, and an interaction between oscillation number and stiffness, $F(3, 184) = 8.15$, $ps < .001$, as shown in Figure 7. Although the interaction indicates the stiffness effect was substantially greater for the first oscillation, it remained significant for the second as well, $F(3, 188) = 6.01$, $p < .001$. Oscillation duration also increased monotonically with stiffness, from 139 ms at the lowest value to 168 ms at the highest, a significant effect, $F(3, 184) = 4.76$, $p = .003$. The effect of stiffness on oscillation duration did not differ between first and second oscillations, as indicated by a non-significant interaction between stiffness and oscillation number.

Discussion

Humans routinely execute controlled, spatially directed actions such as pointing or reaching to contact. Planning and execution of such actions have been the focus of theories at the mechanical, psychological, and neural levels, which have yielded descriptive “laws” (Fitts, 1954, Lacquiniti et al., 1983), models of planning (Rosenbaum et al., 1995) and underlying neural circuitry (Shadmehr & Krakauer, 2008; Sommer & Wurtz, 2008), and control-theoretic analyses of performance (Franklin & Wolpert, 2011). Less theoretical attention has been paid to actions where force constraints are a critical concern. In this paper, one such action, surface puncture, has been described by a three-stage model that proceeds from physically determined interactions, through decline of force due to biomechanical viscosity, to voluntary control. With the specified error tolerances, the model could be fit to kinematic data from individual trials for almost the entire data set (96%). Moreover, the values of derived parameters matched objective measures where available, including the mass of the device and the time-range for centrally mediated sensory-motor loops.

The neural mechanisms of active braking have been increasingly delineated by using neuro-imaging and brain stimulation in tasks where an already initiated motor response is to be

inhibited. Aron and Poldrack (2006) proposed that terminating a triggered program is effected by a cortical-to-subcortical pathway, through which inhibition originating in the right inferior frontal cortex (rIFC) is transmitted to the subthalamic nucleus in the basal ganglia. If this message travels by a “hyperdirect” pathway (Nambu et al., 2002), initiated actions could be terminated in something on the order of 120 ms, close to the minimum time to the deviation point found here (mean 134 ms for pull at maximum stiffness). The critical role of the rIFC area is indicated by the finding that its deactivation through transcranial magnetic stimulation effectively impedes people's ability to stop an ongoing action (Chambers, et al. 2006). Further work indicates that the rIFC-initiated inhibition is mediated by the supplementary motor complex, which includes the pre-supplementary area (Neubert et al., 2010; Zandbelt et al., 2013).

The present model offers insights into how puncture is affected by an important physical parameter of the environment, the stiffness of the penetrated surface, which had far-ranging effects on post-penetration behavior. The results show that stiffer surfaces led to higher initial force, acceleration and velocity; longer stopping times and distances despite a smaller time constant for force decay; and higher-intensity oscillations, although not a greater number, during active braking. In contrast, stiffness as manipulated here had essentially no influence on the inertial mass of the person-device coupling at puncture. We note, however, that this invariance may not hold with a platform that is lower in mass relative to the person holding the tool.

Other variations on the present experiment would be useful to explore factors that affect the kinematics of puncture. A valuable addition would be visual cues to puncture, which would likely alter the velocity of approach to the membrane boundary and might also change arm posture. A more complex model of the membrane would also be of interest, as the present model is intended to capture only the effects of abrupt release of resisting force and reduction in damping.

Pulling motion exhibited more effective braking by several measures in the present data. Relative to pushing, movement in the pull direction led to faster decline of velocity as measured directly and by the parameter, a shorter distance moved at the zero crossing of velocity, and earlier active braking onset as measured by deviation from the force-decay model. While the difference was not significant, pull motions also led to a higher average estimate of inertial mass. These effects collectively indicate that the posture and grip used in pulling led to greater control over the tool/membrane interaction. While the mechanisms behind this effect cannot be specified here, measurement of forearm muscle activation suggests more broadly distributed increases under pull than push (Di Dimizio & Keir, 2010). The more effective braking for pull can be attributed as well to differential impedance setting, presumably under active control in anticipation of task demands (Tsuji et al., 2004). The measured hand and arm impedance, that is, the resistance to disturbance as it reflects inertia, stiffness and viscosity, has been found to be affected by posture (Tee et al., 2004; Mussa-Ivaldi et al., 1985), including gripping actions with a stylus (Fu & Cavuso lu, 2012).

Parameters derived from the present modeling approach characterize an individual's interaction with a surface in terms of inertial mass, time-course of viscous force decline, onset of active braking, and subsequent oscillations. In the present study, parameter values were derived for a healthy population of young adults, who demonstrated very consistent behavior. The same approach might be extended to characterize individuals who have sensory-motor impairments, while using precise parameterization that separates physically determined, biomechanical, and cortically mediated components of motor behavior. Parameters extracted from the model could also be used to describe change over time, for

example, to monitor progression of diseases like Parkinson's Syndrome or neural regrowth after limb transplant.

This research can also potentially be applied to tasks where precise force control is critical, such as eye surgery. In procedures like corneal keratectomies, canalostomy for glaucoma, or retinal repair, interaction forces between the surgical tool and tissue are unpredictable and difficult to detect, if not actually below the sensory threshold (Gupta et al., 1999; Jagtap & Riviere, 2004). Several research groups, including the present authors, have developed devices to amplify forces during surgery (Stetten et al., 2011; Salcudean & Yan, 1994; Taylor et al., 1999; Fleming et al., 2008). While force augmentation has positive effects on sensory detection, the present research also points to potential problems in controlling stopping behavior. The results highlight the potential value of applications that could monitor puncture and actively intervene to correct such problems.

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Figure 1. Behavior of the model (left: distance/time relation; right: velocity/time relation) under varying parameters of stiffness (K) and exponential time constant (τ).

Figure 2.

Distance (left panels) and velocity (right panels) over 500 ms after burst through the simulated membrane for sample trials at two levels of stiffness (K). The black circle indicates the time at which deviation from the exponential-force-decay model was detected.

Figure 3. Stopping efficacy, as indicated by distance from the membrane at the first zero crossing of velocity and time to reach that zero crossing, for four values of stiffness and the two directions of movement. Error bars represent ± 1 standard error.

Figure 4.

Relation between initial acceleration and the force at burst, as controlled by the membrane simulation for four levels of stiffness. Data are shown for two directions of movement along with least-squares fits with intercept forced to zero. Error bars represent ± 1 standard error.

Figure 5.

Values of two time measures, τ and deviation from the model, at four levels of stiffness and the two directions of movement. Error bars represent ± 1 standard error.

Figure 6.

Representative data for distance from the point where behavior deviated from the exponential force-decay model, over 500 ms after deviation, for four trials with different values of stiffness (K), as indicated. As an oscillation is defined by three reversals of direction, there is one oscillation in each trial except for $K = 1130$, which exhibits two.

Figure 7.
Amplitude of first and second oscillation for trials with two oscillations, for four levels of stiffness.