

RESEARCH ARTICLE | *Control of Movement*

Visual perception of joint stiffness from multijoint motion

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Huber ME, Folinus C, Hogan N. Visual perception of joint stiffness from multijoint motion. *J Neurophysiol* 122: 51–59, 2019. First published April 24, 2019; doi:10.1152/jn.00514.2018.—Humans have an astonishing ability to extract hidden information from the movements of others. For example, even with limited kinematic information, humans can distinguish between biological and nonbiological motion, identify the age and gender of a human demonstrator, and recognize what action a human demonstrator is performing. It is unknown, however, whether they can also estimate hidden mechanical properties of another's limbs simply by observing their motions. Strictly speaking, identifying an object's mechanical properties, such as stiffness, requires contact. With only motion information, unambiguous measurements of stiffness are fundamentally impossible, since the same limb motion can be generated with an infinite number of stiffness values. However, we show that humans can readily estimate the stiffness of a simulated limb from its motion. In three experiments, we found that participants linearly increased their rating of arm stiffness as joint stiffness parameters in the arm controller increased. This was remarkable since there was no physical contact with the simulated limb. Moreover, participants had no explicit knowledge of how the simulated arm was controlled. To successfully map nontrivial changes in multijoint motion to changes in arm stiffness, participants likely drew on prior knowledge of human neuromotor control. Having an internal representation consistent with the behavior of the controller used to drive the simulated arm implies that this control policy competently captures key features of veridical biological control. Finding that humans can extract latent features of neuromotor control from kinematics also provides new insight into how humans interpret the motor actions of others.

NEW & NOTEWORTHY Humans can visually perceive another's overt motion, but it is unknown whether they can also perceive the hidden dynamic properties of another's limbs from their motions. Here, we show that humans can correctly infer changes in limb stiffness from nontrivial changes in multijoint limb motion without force information or explicit knowledge of the underlying limb controller. Our findings suggest that humans presume others control motor behavior in such a way that limb stiffness influences motion.

action understanding; dynamic primitives; joint stiffness; motor control; motor perception

INTRODUCTION

We often take for granted how readily we can physically interact with objects in our environment, including simple

objects and highly complex systems like other human beings. Humans can seamlessly shake hands and collaboratively manipulate objects with one another, making it easy to underrate the complicated control problem that physical interaction poses to the central nervous system. The challenge of controlling physical interaction arises from the fact that, when you apply forces on an external object, the object simultaneously applies forces back onto you. The object's dynamics are coupled to your dynamics, and this can destabilize the physically coupled hand-object system. Extensive prior work suggests that humans are able to ensure robust stability during physical interaction by modulating the mechanical impedance of their limbs (i.e., the generalized relation between force and motion) (e.g., Burdet et al. 2001; Damm and McIntyre 2008; Hogan 1984; Lacquaniti and Maioli 1989; Rancourt and Hogan 2009; Senot et al. 2016; Won and Hogan 1995). However, it is still unknown how humans determine the appropriate limb mechanical impedance (e.g., inertia, stiffness, and damping properties) for a particular interaction task since it depends not only on the task but also on the mechanical properties of the object or system with which the interaction is planned.

Strictly speaking, identification of an object's mechanical properties, such as stiffness, requires contact and physical interaction. However, it has been shown that humans can use a multitude of visual cues to deduce these properties of objects before contact. For example, humans can use motion cues to determine the elasticity of a ball from visually observing it bounce on a surface (Nusseck et al. 2007; Warren et al. 1987). They can also infer the stiffness of a static object based on how it deforms in response to external forces (Bouman et al. 2013; Paulun et al. 2017). Even in the extreme case when an object is static and not subjected to external forces, humans can still estimate its stiffness from its optical material properties (e.g., shininess, transparency) drawing from prior experience (Schmidt et al. 2017).

Cooperative physical interaction with another human, however, is much more challenging. Unlike the objects used in these prior studies, humans have actuators (in the form of muscles) and skeletal "redundancy" (more degrees of freedom than the minimum required to position the hand or foot) that allow them to actively control their limb impedance. However, humans have a remarkable ability to extract information from visually observing the motion of others (for review, see Blake and Shiffrar 2007). For instance, humans can distinguish between biological and nonbiological motion (e.g., Johansson 1973), identify the gender of a human demonstrator

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(e.g., Kozlowski and Cutting 1977), and recognize what action a human demonstrator is performing (e.g., de la Rosa et al. 2014; Dittrich 1993). The open question is, can humans also infer the impedance of a human limb without physically interacting with it?

The purpose of this study was to determine if humans can estimate the stiffness of a moving arm without physical contact, i.e., by observing only its kinematic behavior. At first, it might seem implausible that humans could estimate the stiffness of a moving limb without physical interaction. When observing another person, one can visually perceive their overt motion, but it is impossible to unambiguously quantify limb stiffness from motion alone. Additional force information from physical interaction is required to make an accurate measurement. Moreover, the features that generate a particular limb stiffness, such as muscle coactivation or neuromotor commands, are not visible (Brass and Heyes 2005).

However, it is feasible that humans could estimate limb stiffness from motion without physical contact if the following two criteria are met. First, the observed limb must be controlled in such a way that limb stiffness and motion are linked. Note that this limits the possible control architectures. For instance, a typical industrial robot arm can generate practically any nominal motion using high-precision motion control, but its stiffness will be unwaveringly high across all motions and largely independent of them. Second, humans must have sufficient knowledge of the controller to map changes in limb motion to changes in stiffness.

With a series of three experiments, we tested whether humans could perceive changes in limb stiffness of a simulated two-link planar arm. We first simulated human-like arm motions devoid of physical interaction using a controller in which varying joint stiffness influenced motion. We then instructed participants to watch simulated motions of the two-link planar arm and rate “arm stiffness” on a numerical scale. In each experiment, different joint stiffness parameters were varied, which led to distinct changes in arm motion. This allowed us to test how robustly subjects could estimate joint stiffness across different sets of motion patterns.

In all three experiments, we found that participants linearly increased their arm stiffness rating with the simulated joint stiffness, regardless of the affected joint(s) and seemingly nonintuitive changes in motion. This indicates that participants 1) assumed that overt motion is influenced by joint stiffness and 2) had prior knowledge of the controller used to simulate the arm motion. These results are the first demonstration that humans can extract limb impedance information from visually observing its motion, providing new insight into how humans interpret, assess, and learn from the motion of others for physical interaction.

METHODS

Participants. Ten participants took part in each of the three experiments (30 participants in total: 14 males and 16 females with a mean age of 22 ± 4 yr). Participants had a variety of educational backgrounds, including engineering, computer science, material science, and biology. None had any prior experience with the experimental task, and each only participated in one experiment. All participants gave informed written consent before the experiment. The experimental protocol was reviewed and approved by the Institutional Review Board of the Massachusetts Institute of Technology.

Experimental task. In all three experiments, participants viewed a series of simulated arm motions displayed on a computer screen (Fig. 1). In each trial, participants saw a two-link planar arm move its “hand” (endpoint) along an orbital path for 20 s. The hand path was not explicitly displayed. At the end of the simulated motion, participants were instructed to rate “arm stiffness” on a numeric scale from 1 to 7. A rating of 1 indicated that the arm was “least stiff,” and a rating of 7 indicated that the arm was “stiffest.” After submitting a rating, participants self-initiated the next trial, allowing them to take a break at any time if needed.

Each participant performed 30 trials. Participants were shown six unique arm motions that were repeated five times in a blocked manner. The order was randomized within each block. The whole experiment lasted ~20 min.

A custom graphical user interface developed in MATLAB (The MathWorks, Natick, MA) was used to conduct the experiment, including simulating and displaying the arm motions and recording the arm stiffness ratings.

Simulated arm motions. The simulated arm motions were intended to represent actual human motor behavior. The arm was modeled as a two-link planar manipulator moving in the vertical plane. The dynamics of this model were described as

$$M(q)\ddot{q} + C(q, \dot{q})\dot{q} + g(q) = \tau$$

where $q, \dot{q}, \ddot{q} \in \mathbb{R}^{2 \times 1}$ are the joint angular positions, velocities, and accelerations, respectively, $M(q) \in \mathbb{R}^{2 \times 2}$ is the inertia matrix, $C(q, \dot{q}) \in \mathbb{R}^{2 \times 2}$ are the Coriolis and centrifugal terms, $g(q) \in \mathbb{R}^{2 \times 1}$ are the gravitational terms, and $\tau \in \mathbb{R}^{2 \times 1}$ are the commanded joint torques. The length, mass, center of mass, and moment of inertia parameters for the two links were chosen to match the forearm and upper arm of an average male human as described previously (Zatsiorsky 2002).

The controller driving the simulated arm was consistent with a proposal that human motor behavior is composed of dynamic primitives (Hogan 2017; Hogan and Sternad 2012). In the simulation the controller comprised two components. One, a combination of an oscillatory primitive with mechanical impedance in hand coordinates, acted to pull its endpoint along a circular path. At the same time, the other, a combination of a fixed-point primitive with mechanical impedance in joint coordinates, acted to pull it to a nominal joint



Fig. 1. Experimental setup. In each trial, participants viewed a two-link planar arm moving periodically for 20 s on a computer screen. After watching the simulated arm motion, participants rated arm stiffness on a numeric scale.

configuration or pose. The commanded joint torques were determined by

$$\tau = J(q)^T K_x (x_r - x) - J(q)^T B_x \dot{x} + K_q (q_r - q)$$

$$x_r = \begin{bmatrix} 0.1 \cos\left(\frac{20t}{3}\right) \\ 0.1 \sin\left(\frac{20t}{3}\right) \end{bmatrix}, q_r = \begin{bmatrix} \frac{\pi}{4} \\ \frac{\pi}{4} \end{bmatrix}$$

$$K_x = \begin{bmatrix} 500 & 0 \\ 0 & 500 \end{bmatrix}, B_x = \begin{bmatrix} 10 & 0 \\ 0 & 10 \end{bmatrix}, K_q = \begin{bmatrix} S & 0 \\ 0 & E \end{bmatrix}$$

where $x, \dot{x} \in \mathbb{R}^{2 \times 1}$ were the endpoint (i.e., hand) positions and velocities, respectively; $J(q) \in \mathbb{R}^{2 \times 2}$ was the Jacobian matrix; x_r was the reference endpoint position, which followed a circular path; q_r was the reference joint configuration; K_x and B_x were the endpoint stiffness and damping matrices, respectively; K_q was the joint stiffness matrix; and $S, E \in \mathbb{R}_{\geq 0}$ were the values in the joint stiffness matrix corresponding to the shoulder and elbow joints, respectively.

In *experiment 1*, the six unique arm motions were generated by setting $S = E = \{0, 10, 20, 30, 40, 50\}$ Nm/rad (Fig. 2A). The range of elbow and shoulder stiffness values used is similar to those reported in human studies (Bennett et al. 1992; Lacquaniti et al. 1982; Mussa-Ivaldi et al. 1985). In *experiment 2*, the motions were generated by setting $E = \{0, 10, 20, 30, 40, 50\}$ Nm/rad and $S = 0$ Nm/rad (Fig. 2B). In *experiment 3*, the motions were generated by setting $S = \{0, 10, 20, 30, 40, 50\}$ Nm/rad and $E = 0$ Nm/rad (Fig. 2C). Prior human studies have shown that humans are capable of

independently modulating shoulder and elbow stiffness (Franklin et al. 2007; Gribble and Ostry 1998; Perreault et al. 2002).

Task instructions. In this study, we took several precautions to ensure that participants did not know how the simulated arm was controlled. Most importantly, we did not want participants to know that we were manipulating joint stiffness, let alone which joint was being manipulated. Thus, we purposefully used the vague term arm stiffness when instructing participants to rate the simulated arm motions. In the event that a participant was unsure of what the term stiffness meant, they received the following definition: “Stiffness is the extent to which an object resists deformation or deflection in response to an applied force. A stiffer object has higher resistance to deflections than a less stiff object.” This instruction was only provided to two participants. Participants were not presented with examples of “more” and “less” stiff arm motions before the experiment. We also purposefully did not provide subjects with any details regarding the controller. They were not told the reference endpoint trajectory was circular, and they saw neither it nor the reference joint pose at any point in the experiment. Last, we did not tell subjects the plane in which the arm was moving. Unbeknownst to the participants, the arm was moving in the vertical plane and subject to gravitational forces.

After completing the experiment, subjects were asked to verbally describe their strategy for estimating arm stiffness.

Statistical analysis. In all experiments, we hypothesized that subjects would linearly increase their arm stiffness rating with the simulated joint stiffness. To test this hypothesis, we conducted a 6 (joint stiffness) \times 4 (block) ANOVA on the arm stiffness rating for each experiment. Joint stiffness and block were within-subject factors. The Greenhouse-Geisser correction was applied to these factors.

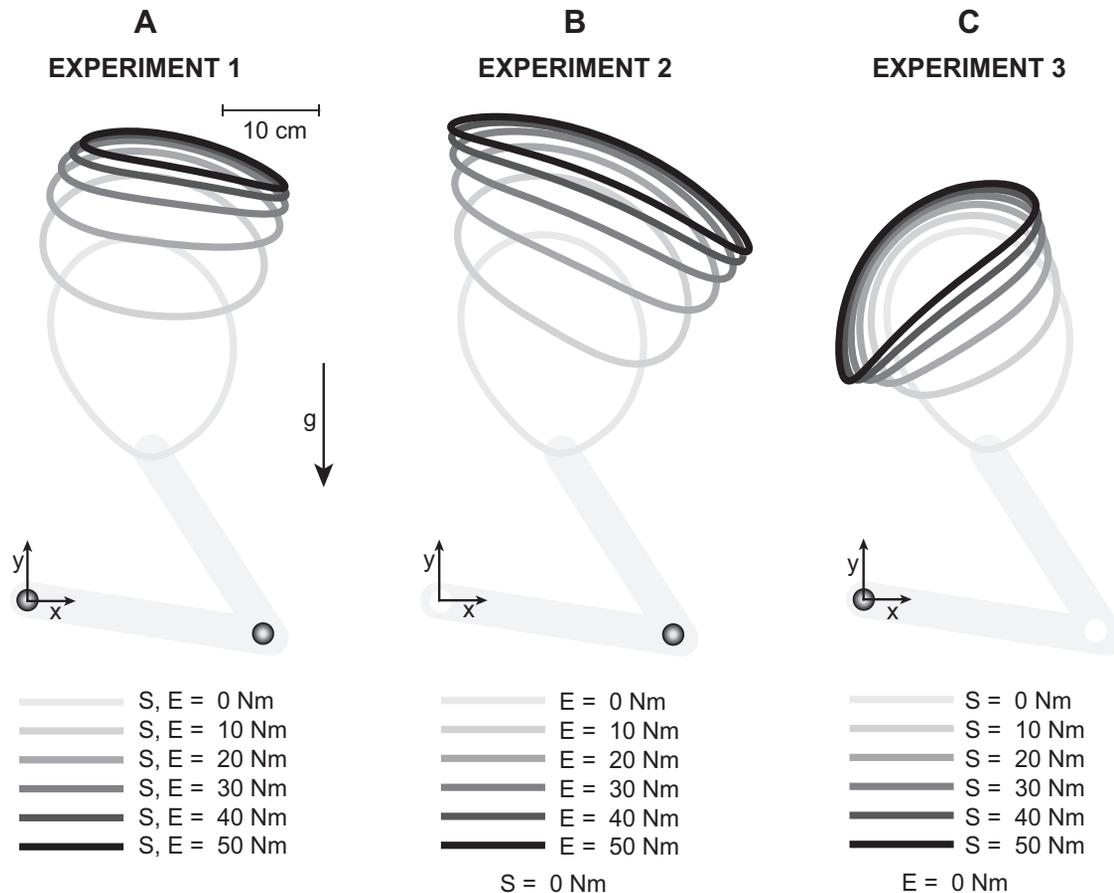


Fig. 2. Six endpoint motions of the simulated arm in each experiment. A: in *experiment 1*, both elbow and shoulder stiffness were varied simultaneously. B: in *experiment 2*, elbow stiffness (E) was varied, and shoulder stiffness (S) was set to zero. C: in *experiment 3*, shoulder stiffness was varied, and elbow stiffness was set to zero. During the experiments, participants only saw the moving limb and were not shown the endpoint traces portrayed here.

Because it was difficult for subjects to gauge relative stiffness ratings in the beginning of the experiment, the arm stiffness ratings from the first block of trials were excluded from all statistical analyses. A subsequent analysis showed that omitting this first block had minimal effect on the results and did not change the significance of any effects or interactions. A planned polynomial trend analysis was also conducted to further test whether the effect of joint stiffness on arm stiffness rating was linear.

To further investigate the potential strategies subjects used to rate stiffness, we tested for differences in stiffness rating variability across joint stiffness conditions. Specifically, a 6 (joint stiffness) \times 3 (experiment) ANOVA was conducted on the SD of arm stiffness rating, where joint stiffness condition was a within-subjects factor and experiment was a between-subjects factor.

In all statistical tests, the significance level was set to $P < 0.05$. Statistical analyses were performed using SPSS Statistics for Windows, version 24.0 (IBM, Armonk, NY).

RESULTS

Figure 3 shows the raw data from individual participants in all experiments with linear fits for visualization. The majority of individual participants across all experiments increased arm stiffness rating as simulated joint stiffness was increased.

Experiment 1: changing elbow and shoulder stiffness. The ANOVA revealed a significant main effect of simulated joint stiffness on arm stiffness rating [$F(1.29,11.59) = 6.20$; $P = 0.023$, partial $\eta^2 = 0.41$] (Fig. 3A). Moreover, the effect of simulated joint stiffness on arm stiffness rating was linear [$F(1,9) = 7.39$; $P = 0.024$, partial $\eta^2 = 0.45$]. As hypothesized, subjects linearly increased their arm stiffness rating as simulated elbow and shoulder joint stiffness were increased (Fig. 4).

There was no significant effect of block [$F(2.02,18.15) = 1.11$, $P = 0.35$, partial $\eta^2 = 0.11$] nor an interaction [$F(4.40,39.63) = 1.02$, $P = 0.41$, partial $\eta^2 = 0.10$]. Participants did not “learn” or alter their rating strategy as the experiment progressed.

Experiment 2: changing elbow stiffness. Consistent with the results of *experiment 1*, participants linearly increased their arm stiffness ratings with increased elbow stiffness as hypothesized. The ANOVA revealed a significant main effect of elbow stiffness on arm stiffness rating [$F(2.33,21.00) = 33.10$; $P = 1.43 \times 10^{-7}$, partial $\eta^2 = 0.79$] (Fig. 3B), and again, the effect was linear [$F(1,9) = 70.10$, $P = 1.50 \times 10^{-5}$, partial $\eta^2 = 0.89$] (Fig. 4). There was no significant effect of block [$F(2.43,21.89) = 0.022$, $P = 0.99$, partial $\eta^2 = 0.02$] nor an interaction [$F(5.21,46.85) = 1.01$, $P = 0.42$, partial $\eta^2 = 0.10$].

One subject, who happened to be a trained physical therapist, performed exceptionally well (highlighted in Fig. 3B). To test whether this subject’s performance skewed our results, the statistical analysis was repeated without this subject’s data. We observed that excluding this subject had only a minimal effect on the statistical results [elbow stiffness: $F(2.20,17.58) = 26.47$, $P = 3 \times 10^{-6}$, partial $\eta^2 = 0.77$; linear effect of elbow stiffness: $F(1,8) = 56.37$, $P = 6.9 \times 10^{-5}$, partial $\eta^2 = 0.88$; block: $F(2.43,19.48) = 0.004$, $P = 0.99$, partial $\eta^2 = 4.50 \times 10^{-4}$; elbow stiffness \times block: $F(5.06,40.49) = 0.96$, $P = 0.46$, partial $\eta^2 = 0.11$]. Importantly, the significance of the effects and interactions was unchanged.

Experiment 3: changing shoulder stiffness. Participants also increased their arm stiffness ratings with increased shoulder stiffness as hypothesized. The ANOVA revealed a signifi-

cant main effect of shoulder stiffness on arm stiffness rating [$F(1.64, 14.80) = 9.62$, $P = 0.0031$, partial $\eta^2 = 0.52$] (Fig. 3C), which was linear [$F(1,9) = 14.42$, $P = 0.0042$, partial $\eta^2 = 0.62$] (Fig. 4). There was no significant effect of block [$F(1.72,15.43) = 0.10$; $P = 0.88$, partial $\eta^2 = 0.01$], nor an interaction [$F(3.61,32.49) = 0.61$, $P = 0.64$; partial $\eta^2 = 0.064$].

Effect of simulated joint stiffness condition on stiffness rating variability. To assess whether participants could distinguish any of the motion patterns better than the others, we examined the variability in stiffness rating across the different joint stiffness conditions. It was plausible, for instance, that participants might identify the motion pattern in the zero joint stiffness condition more readily than in the others, since it most closely resembled a circular motion (Fig. 2, A–C). Participants could have used deviation from the motion pattern in the zero joint stiffness condition as a strategy for estimating joint stiffness across the other conditions. However, an ANOVA revealed no significant main effects of joint stiffness or experiment, nor an interaction, on stiffness rating variability [joint stiffness: $F(4.48,120.81) = 1.57$, $P = 0.18$, partial $\eta^2 = 0.06$; experiment: $F(2,27) = 1.16$, $P = 0.33$, partial $\eta^2 = 0.07$; joint stiffness \times experiment: $F(8.95,120.81) = 0.99$, $P = 0.44$, partial $\eta^2 = 0.08$] (Fig. 5). Thus, identifying and subsequently measuring deviation from the endpoint motion pattern in the zero joint stiffness condition does not appear to be the dominant strategy used by subjects.

DISCUSSION

This study tested whether humans could perceive changes in joint stiffness from strictly overt motion. We found that participants linearly increased their arm stiffness rating with simulated joint stiffness in all experiments. Unambiguously measuring impedance properties, such as stiffness, fundamentally requires an object to undergo physical interaction. Because the simulated arm did not experience mechanical contact in the experimental task, it was remarkable that participants could still successfully judge changes in joint stiffness from motion. To our knowledge, these results are the first demonstration that humans can perceive stiffness of an actuated system with a human-like controller from visually observing its motion.

While participants overall were successful at this task, individuals did vary in their ability to rate arm stiffness accurately (Fig. 4). Such variability is typical in human motor and perception experiments and can have a variety of origins. One common source of interparticipant variability in motor experiments is prior experience or training. Investigating whether training in motion perception, or even skilled motion generation, influenced rating performance was beyond the scope of this study. Nevertheless, our experimental results suggest that this may be a fruitful area for further research and support the speculation that prior experience could have been a factor. For instance, the participant who performed the best (i.e., had the best linear fit between joint stiffness and arm stiffness rating) was a practicing physical therapist (highlighted in Fig. 3B) whose training included observing human motion and diagnosing abnormalities in “muscle tone.” It also worth noting

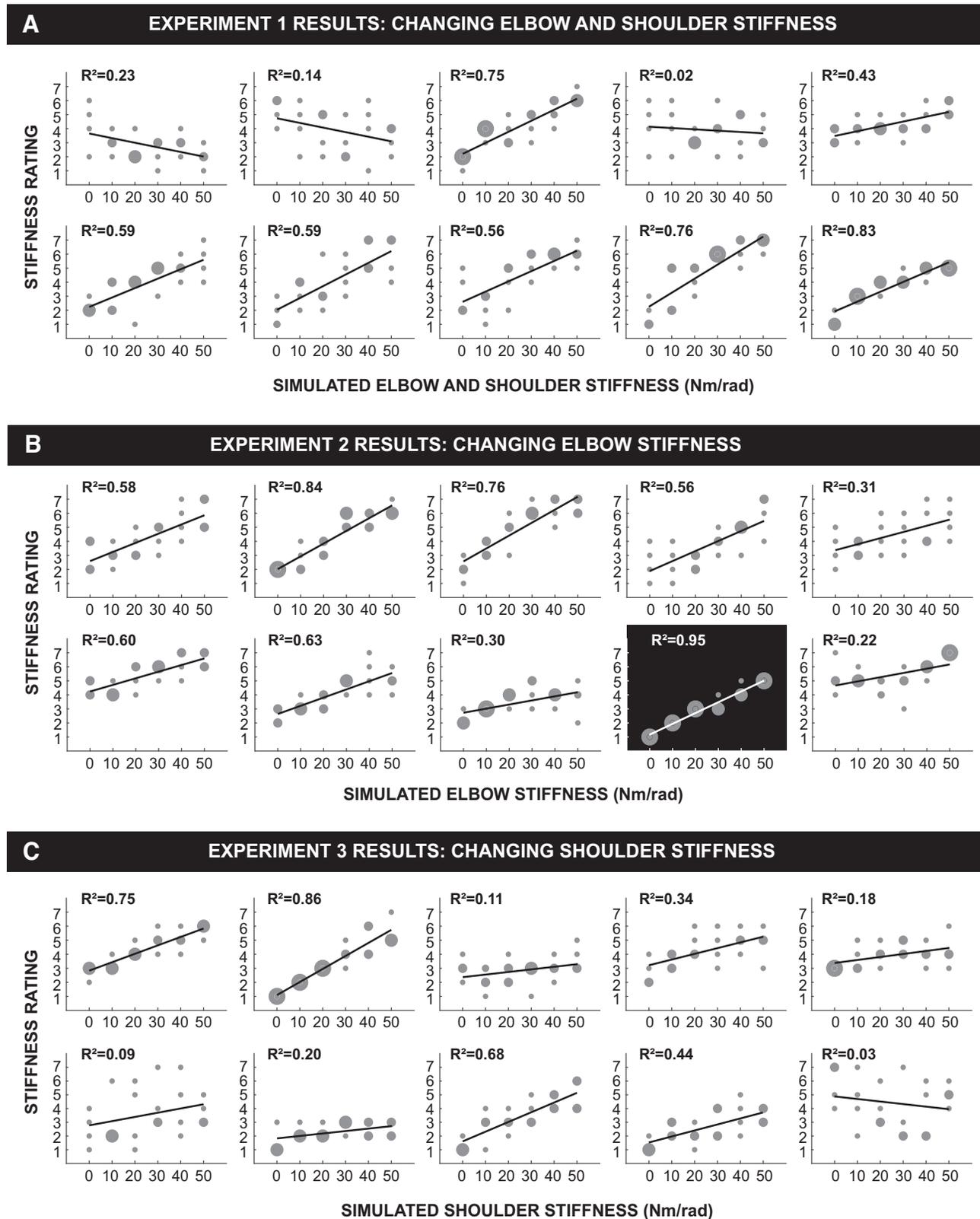


Fig. 3. Raw data of each participant's arm stiffness ratings across simulated joint stiffness values in *experiment 1* (A), *experiment 2* (B), and *experiment 3* (C). Note that data from the first block are omitted since it was not included in subsequent statistical analyses. Larger dots indicate a greater response frequency. The black lines represent the linear fit of each participant's data. Participant datum highlighted in black was a trained physical therapist.

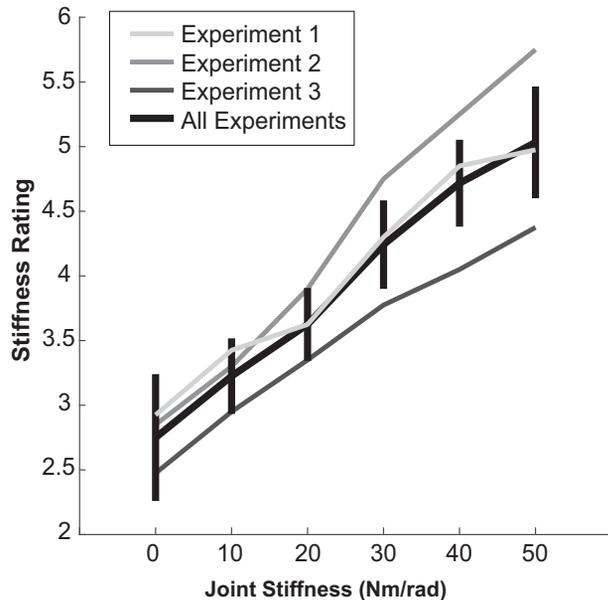


Fig. 4. Stiffness rating results. In all three experiments, there was a significant positive linear effect of joint stiffness on the arm stiffness ratings. Thin lines, average arm stiffness rating across participants within each experiment; thick line, average stiffness rating across participants in all experiments. Error bars represent ± 2 SEs.

that the participants with formal training in the meaning of stiffness and its importance in dynamics and controls (e.g., engineers) did not outperform those without it. Although it remains to be tested, this suggests that experiential, not mathematical, knowledge of the concept of stiffness may influence one's ability to estimate it from motion.

It is also possible that some of the interparticipant variability resulted from the experimental protocol. For instance, the task instructions were purposefully vague so as not to give participants any information about how the arm was controlled. Participants might have interpreted the meaning of arm stiffness differently, which would influence their rating strategies. Even if participants asked for additional clarification of the term arm stiffness, we only provided a definition of "stiffness" and instructed participants to try their best at the task. While this vague instruction avoided introducing bias into the participants' ratings, it also opened the possibility for participants to rate or estimate some variable other than the stiffness parameter altered in our controller. Still, it was our utmost priority not to unknowingly signal to participants how the arm was being controlled.

The use of a numerical scale to quantify participants' ratings of arm stiffness could have also introduced measurement error. Such error is analogous to quantization error, which arises when representing a continuous analog signal with discrete stepped digital data (Bennett 1948). Quantization error can be modeled as uniformly distributed noise with a mean of zero and a variance that depends on the resolution of the digital representation. In this task, the variance of the error depends on the resolution of the numeric scale (i.e., the number of rating options); the greater the number of rating options, the lower the noise. One well-known limitation of Likert-type scales is that they are vulnerable to response bias, which occurs whenever a person responds systematically on some basis other than what the items were specifically designed to measure. As seen in

Figs. 3 and 4, not all participants used the full range of the numeric scale. This form of response bias results in greater noise and seemingly worse performance than if the full range had been used.

Even though several aspects of the experimental protocol may have induced a portion of the observed interparticipant variability, the effect of these factors would have made performing the task harder, not easier, for participants. Despite the possibility that these factors could have increased the task difficulty, the majority of individual participants were nevertheless successful.

In these experiments, there were a multitude of motion-related cues that participants could have used to estimate stiffness. Figure 6, A–F, shows how a subset of such features varied with joint stiffness in each of the three experiments. There were cues, both temporal and spatial, that changed consistently with increased joint stiffness in all three experiments. These include the oblongness (Fig. 6A) and area (Fig. 6B) of endpoint path, the relative phase between the shoulder and elbow motion (Fig. 6C), and shoulder range of motion (Fig. 6E). However, not all features changed consistently across the three experiments, such as the relative phase between endpoint motion in the x and y directions (Fig. 6D) and elbow range of motion (Fig. 6F). The fact that participants performed equally well in all experiments suggests that they might be using features that varied consistently across experiments to estimate stiffness although it is equally possible that participants integrated several different motion cues to estimate stiffness.

After performing the experiment, we asked participants to describe what motion-related cues they used to determine their rating. However, their verbal responses were often inscrutable. In general, participants reported using at least some aspect of

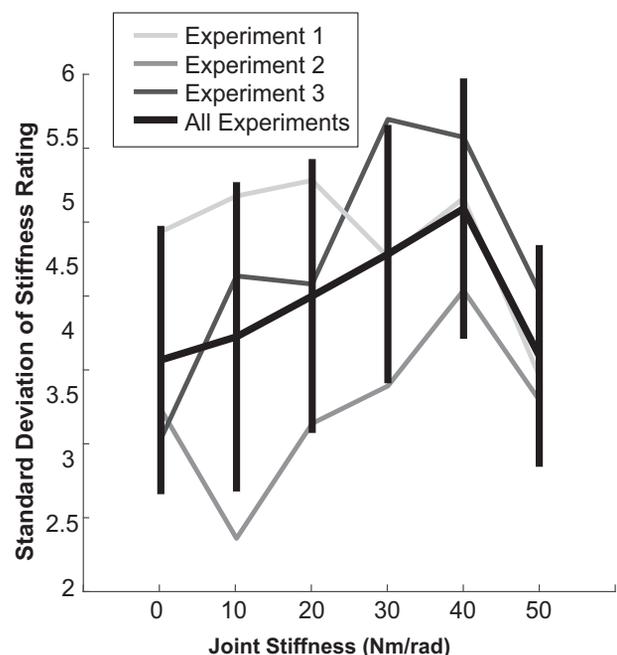


Fig. 5. Variability in stiffness rating results. In all three experiments, there was no effect of joint stiffness or experiment, nor an interaction, on the SD of stiffness ratings. Thin lines, average SD of stiffness rating across participants within each experiment; thick line, average SD stiffness rating across participants in all experiments. Error bars represent ± 2 SE.

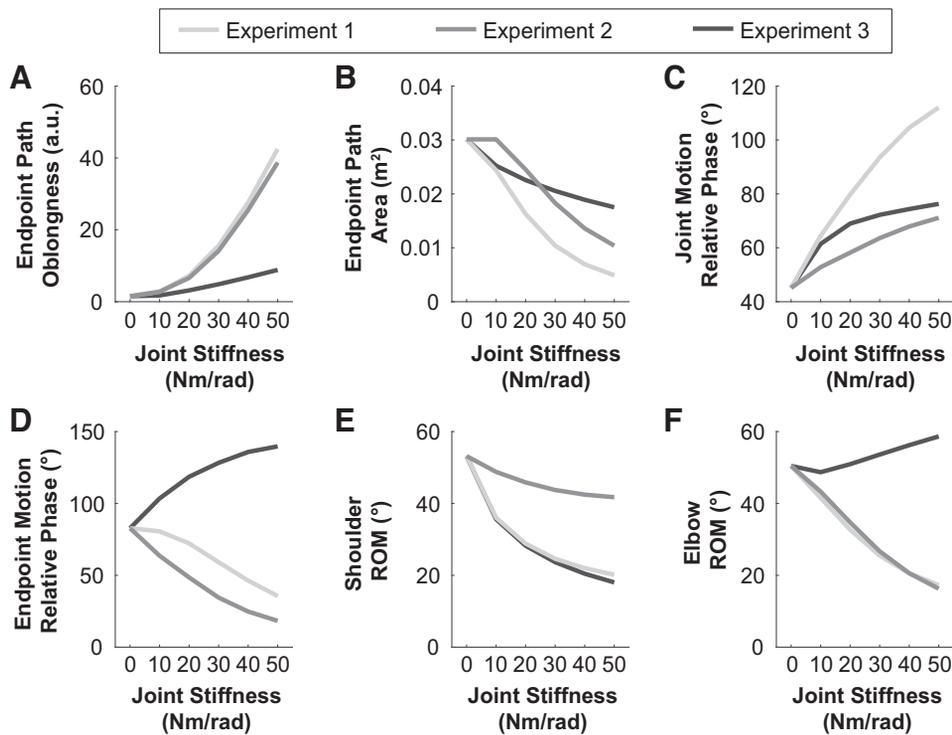


Fig. 6. Change in motion-related features with change in simulated across all experiments. *A*: endpoint path oblongness was defined as the ratio of the eigenvalues of the covariance matrix for the endpoint path in Cartesian coordinates. *B*: endpoint path area was defined as the area enclosed by the endpoint path in Cartesian coordinates. *C*: joint motion relative phase was defined as the relative phase between the elbow and shoulder motion and was calculated using cross-correlation analysis. *D*: endpoint motion relative phase was defined as the relative phase between the endpoint motion in Cartesian coordinates and was similarly calculated using cross-correlation analysis. *E* and *F*: shoulder (*E*) and elbow (*F*) range of motion (ROM).

joint motion, such as joint range of motion or relative velocity between the joints, but often their description of the cues was inexact and vague. Interestingly, none mentioned the term “endpoint” or “hand position” when describing their rating strategy, but it is possible they used this knowledge unknowingly. Although this debrief did not shed light on what motion-related cues were used as criteria for rating stiffness, it does suggest that participants did not use explicit conscious strategies. This is consistent with the notion that observational motor learning may be an implicit process (Mattar and Gribble 2005).

Because subjects could not articulately communicate their rating strategy, we also examined variability to further probe how subjects determined their stiffness rating. However, we found no effect of joint stiffness on stiffness rating variability in the three experiments (Fig. 5), indicating that participants were not able to identify the motion pattern from one condition more readily than the others.

Even though we were unable to identify how participants were able to estimate stiffness from motion, our results strongly indicate that participants did not perform the task by simply reporting changes of some observable motion variable(s) and randomly “guessing” how it related to the latent variable of joint stiffness. If such a strategy was used, we would expect some participants to have exhibited a negative relationship between arm stiffness rating and simulated joint stiffness. Even though they varied in their ability to perform the task, none had a significant negative relationship between arm stiffness rating and simulated joint stiffness in any of the experiments (Fig. 3). Moreover, participants were not given feedback as to whether their ratings were correct nor did they change their rating performance over the course of the experiment. Thus, participants did not have opportunity to learn the relation between motion and stiffness in a supervised manner, although it is possible that they could have learned this relation in an unsupervised manner. However, we did not observe a

significant effect of block in any of the experiments. This suggests that either no learning occurred or that the effect of learning in this experiment was very small, perhaps because the timescale for learning in this task might be much longer than the duration studied in this experiment.

To successfully perform the perception task, participants likely drew on prior knowledge that was consistent with the behavior of the controller used to drive the simulated arm. How did participants have a competent internal representation of the control policy used to drive the simulated arm? The most likely explanation is that participants drew from their implicit knowledge of human neuromotor control to perform the perception task. In fact, the controller used in the simulation was specifically chosen to mimic important features of human neuromotor control, in particular the influence of mechanical impedance.

On its surface, motion control can be an enticing account for how the human nervous system produces motor behavior. With this form of control, motion errors between the executed and planned behavior are as small as the limitations of sensing, actuation, and computation accuracy will allow. For instance, it is well documented that humans tend to perform smooth straight line reaching movements (Flash and Hogan 1985). Even when the hand path is subject to visual distortion (Flanagan and Rao 1995) or mechanical perturbations (Lackner and Dizio 1994; Shadmehr and Mussa-Ivaldi 1994), humans adapt their behavior to restore the original straight smooth path. These results suggest that neuromechanical dynamics are subservient to kinematics, which is the behavior one would expect to arise from a motion controller. As previously mentioned, however, this type of motion control uncouples the executed motion trajectory from joint stiffness.

In addition, prior research has shown that even those seemingly straight reaching movements are influenced by limb impedance. Although close to optimal, human reaching move-

ments are not ideally straight. As observed by Flash (1987), these movements are slightly curved, and the curvature varies depending on the direction of hand movement and the hand position within the workspace. She also demonstrated that these systematic patterns could be reproduced using a control strategy where limb impedance influenced motion. Specifically, the controller used in Flash (1987) had the hand track an optimally straight hand trajectory with stiffness values derived from human measurements (Mussa-Ivaldi et al. 1985). The extent of the curved deviations can be varied by altering the limb impedance.

In line with the experimental results of Flash (1987), Hogan and Sternad (2012) offer a theory of human sensorimotor control wherein limb motion and impedance are coupled. They propose that human motor behavior is encoded solely in terms of attractors (also referred to as dynamic primitives). Motion attractors are combined with mechanical impedance attractors to generate both the desired motion and interactive behavior of the body. Any such controller that implements a motion and a joint impedance primitive will yield a particular kinematic synergy (Hogan and Sternad 2012). By this theory, motions are generated in such a way that they contain limb impedance information that an observer could extract. In the experimental task, it was also crucial to simulate the arm motion such that limb stiffness and motion were linked. It would have been fundamentally impossible for participants to perform the task otherwise. The controller used in this study was built from dynamic primitives using the compositionality of mechanical impedance (Hogan 2017). Specifically, the simulated arm behavior was akin to the superposition of a limit cycle (in hand space) and a point attractor (in joint space), each with its own impedance. This controller is representative of how the nervous system might coordinate the integration of multiple motor behaviors to perform a complex action. Examples of such complex actions are holding books in your arm while simultaneously using that same arm to open a door or using a tool while maintaining standing balance. In the former example, maintaining a particular limb posture with particular levels of tonic muscle activation will impose a joint stiffness and ultimately affect the overt movement pattern (Hogan and Sternad 2012). It should also not be overlooked that, in biological systems, the passive stiffness of muscles and tendons also influences the effective stiffness of the joints.

The evidence suggesting that human upper limb motions are influenced by limb impedance supports the notion that participants used their implicit knowledge of human neuromotor control to perform the perception task. We emphasize, however, that this is not to say that the control policy used to simulate arm motion in this study is the veridical motor controller embedded in the human nervous system. Instead, we only assert that control strategies of this form are representative of how humans generate motion, or at least how they perceive other humans to generate motion. Hence, they may serve as competent descriptive models of human neuromotor control.

Although still an open question, it is also worth considering how such models for perceiving motion could arise. For instance, such models could be built empirically based on prior observations of others (Battaglia et al. 2013). It is also plausible that participants used knowledge of how they control their own motions to interpret the perceived motor actions of others. While controversial, there is evidence to support such a notion

of embodied cognition (Hickok 2009). Neuroimaging evidence suggests humans use their own motor system to recognize and understand the action of others (Dayan et al. 2007; Grafton et al. 1997; Iacoboni et al. 1999). It has been proposed that, by mapping observed actions in the motor system, the observer gains knowledge of how those actions may be controlled internally (Casile and Giese 2006; Giese and Poggio 2003; Rizzolatti et al. 2001). Thus, subjects may have used an internal model or understanding of their own limb dynamics to successfully perform the experimental task. For instance, prior human studies found that visually observing a motor action performed by another individual increased the excitability of the neuromotor system, specifically of the activation of muscles that were involved in the observed action (Aglioti et al. 2008; Fadiga et al. 1995; Romani et al. 2005).

This ability to estimate limb stiffness likely plays an important role in several processes, such as planning physical interaction with another individual or performing cooperative interaction tasks. Our results also suggest that it plays an important role in assessing “movement quality,” such as during physical rehabilitation or athletic performance. However, additional research is needed to assess whether individuals can estimate limb stiffness with different movement types (e.g., discrete movements) and across the different limbs, especially in real world scenarios. In prior work, Mattar and Gribble (2005) have shown that learning to reach in a novel force field is enhanced when subjects first watch another subject learn to perform the task. In their experimental task, learning from observation calls for the observer to estimate limb stiffness. This suggests that visually estimating limb stiffness may be an important aspect of learning from observing the actions and interactions of others.

In conclusion, remarkably, our results indicate that humans can extract limb impedance information from overt motion. Without mechanical contact, to correctly infer joint stiffness from motion, participants likely used prior knowledge consistent with the behavior of the control policy used in this study. Although it remains to be tested, it is likely that humans relied on their prior knowledge of human neuromotor control (either from prior observations or from their own sensorimotor system) to successfully perform the experimental task. Our finding that humans can infer latent features of an underlying controller provides new insight into how humans interpret the motor actions of, and subsequently interact with, others.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

M.E.H. conceived and designed research; M.E.H. and C.F. performed experiments; M.E.H. and C.F. analyzed data; M.E.H., C.F., and N.H. interpreted results of experiments; M.E.H. prepared figures; M.E.H. drafted man-

uscript; M.E.H. and N.H. edited and revised manuscript; M.E.H., C.F., and N.H. approved final version of manuscript.

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