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The influence of intersegmental dynamics on limb position sense

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Abstract

During multijoint limb movement, the motion of limb segments can be driven actively, by muscle torque, and/or passively, by interaction torque–rotational force that arises passively at one joint due to motion of an adjacent limb segment about another joint. Proprioception plays a critical role in compensating for interaction torques, and deafferented patients have marked deficits in this aspect of motor control. This observation is seemingly at odds with the widely-held belief that proprioceptive sense is poor during motion that is not driven by active muscle contraction, and suggests that proprioceptive acuity might be preserved during motion that is driven by interaction torque. We designed a study to determine whether the nature of the torques driving joint motion influences proprioceptive sense at that joint. We quantified proprioceptive acuity at the elbow joint while participants were midway through each of two kinds of reaching movements that both involved elbow extension: one in which extension was primarily driven passively by interaction torques, and another in which extension was primarily driven actively by elbow muscle torques. We delivered equally sized and timed perturbations to the elbow joint during motion. Participants' ability to correctly sense the direction in which the elbow was perturbed (flexion or extension) differed depending on if the perturbation was delivered during interaction torque-driven motion or active muscle torque-driven motion. Specifically, participants had superior perceptual acuity when joint motion was driven by interaction torque, suggesting that proprioceptive sense is preserved during this type of motion.

Keywords: Proprioception, Interaction Torque, Intersegmental Dynamics, Reaching, Sensorimotor, Muscle Spindle, Human, Motor Control, Muscle Torque

Summary for Lay Audience

Proprioception is our sense of limb position. Previous studies have sought to determine if the accuracy of proprioception is different when we are engaged in movements that we generate ourselves (e.g., when reaching towards an object), compared to when we are engaged in movements that we do not generate ourselves (e.g., when someone else is guiding our hand towards an object). In real life, our movements are not usually passively guided by someone else; however, they can be (and often are) driven by forces other than the ones our muscles exert on our limbs to move them. For example, when the right arm is used to reach towards an object that is located to the right of the body, the elbow extends primarily because our elbow extensor muscles are producing forces that rotate the forearm relative to the upper arm—that is, the rotational forces (i.e., torques) driving movement mostly come from our muscles. But when the right arm is used to reach to an object that is located to the left of the body, the elbow's extension is primarily driven by the rotation of the upper arm about the shoulder joint, not by forces exerted by our elbow extensor muscles. Thus, elbow extension can be driven not just by the torque our muscles actively produce, but also by torque that is produced by the passive interactions of limb segments that are attached to each other in the multijoint human arm. This provides the basis for a more naturalistic way to examine whether proprioception differs during movements that we do or do not generate ourselves: in this study, we will compare proprioception at the elbow joint when joint motion does (muscle torque-driven motion) or does not (interaction torque-driven motion) result from the activity of the muscles that are responsible for moving that joint.

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List of Abbreviations

UR	Uncertainty Range
SSE	Sum of Squared Errors
SSE_V	SSE between our velocity-based prediction and the actual trajectory
SSE_C	SSE between the controller’s prediction and the actual trajectory

Chapter 1

1 Introduction

1.1 Proprioception

1.1.1 Proprioception and its Importance for Motor Control

Humans rely on sensory information in order to successfully navigate and interact with the world around us. From seemingly simple tasks such as pointing a finger, to more complex tasks like walking or playing sports, we continuously gather sensory cues about our body and the environment to help plan and execute our movements. One sense that is vital for movement is proprioception (Cordo et al. 1994; Hasan 1992; Rothwell et al. 1982; Sainburg et al. 1999), our sense of body position and movement in space, including limb position sense. One function that our proprioceptive sense serves is as a movement control mechanism. In determining what commands it will send to our muscles to generate a movement, the brain uses information about our current limb and body position in space. Proprioceptive information can also elicit reflexes that maintain postural control in the face of unexpected disturbances. For example, spinal stretch reflexes, initiated by an abrupt and involuntary change in muscle length, can mitigate the consequences of sudden perturbations (Reschechtko and Pruszynski 2020). Proprioceptive information is also used during movement execution. As we move, we continuously receive afferent feedback about the position of our limbs in space. This feedback allows the brain to verify that the commands it sent to our muscles produced their intended sensory consequences, and to adapt the commands it sends to our muscles if we experience any unexpected errors (Miall and Wolpert 1996). For example, on a windy day we might have difficulty accurately reaching out for an object, but proprioceptive feedback might allow the brain to make real-time corrective modifications to our muscle activity so that we can regain control of the reach. The proprioceptive feedback might also inform the commands sent out on future reaches, so that we can avoid experiencing the same error the next time we reach out in the wind. Proprioception thus plays an important role as a movement control mechanism and can act as such without necessarily depending on conscious perception.

Although the role of proprioception in motor control does not necessarily rely on the conscious perception of proprioceptive information, our perception of the position and motion of our limbs and bodies in space allows us to make conscious judgments about our bodies, and contributes to our sense of self-consciousness by allowing us to form and update higher-level (e.g., cognitive) internal representations of the body. Perceiving proprioceptive input can also contribute to movement control. For example, to touch a finger to one’s nose while the eyes are closed involves perceiving the locations of the finger and nose in space, through the use of internal representations of the body and incoming sensory information from proprioceptive receptors.

1.1.2 Neurophysiology of Proprioception: Muscle Spindles

Proprioception is sensed by a number of different mechanoreceptors, termed proprioceptors, that are present in muscles, ligaments, tendons, skin, or joint capsules (Proske and Gandevia 2012). Although the various proprioceptors all provide sensory information, some—namely, muscle spindles—play larger roles than others in mediating our position- and movement-sense.

Muscle spindles are stretch receptors that are found in the body of skeletal muscles. The muscle fibers in a spindle (intrafusal fibers) are oriented parallel to the extrafusal muscle fibers that facilitate muscle contraction. Intrafusal fibers are stretched with the extrafusal muscle, and the amount and velocity of this stretch is signaled by primary and secondary afferents that are coiled around the intrafusal fibers. The stretch-sensitivity of the afferents is modulated by gamma fusimotor nerve fibers, which stimulate the intrafusal fibers and cause them to become taut, increasing the resting firing rate of the afferents and therefore increasing their sensitivity to changes in muscle length (Michael-Titus et al. 2010). Spindles have also been shown to have preferred sensory directions, and the collective responses of multiple spindles produces a population code that encodes direction when a limb undergoes movement (Bergenheim et al. 2000; Jones et al. 2001; Roll et al. 2000, 2004).

Muscle spindles are widely believed to be the principal receptors involved in proprioception. Evidence for this claim includes work that has shown that vibration of muscle tendons produces the illusion of limb movement and altered position (Cordo et al. 1995; Eklund 1972; Goodwin et al. 1972; Kammers et al. 2006; Sittig et al. 1985, 1987), even when cutaneous and joint afferents are removed by anesthetization (Goodwin et al. 1972). This effect is largely mediated by primary spindle endings (Roll et al. 1989; Roll and Vedel 1982). Other work has also established that proprioceptive sense can be maintained following deficits or lesions that affect other proprioceptors but leave spindles intact. For example, Gandevia and McCloskey (1976) found that after anesthetizing the finger such that cutaneous and joint afferents would no longer be intact, tensing the muscles of the finger improved—and in some cases, completely restored—subjects' ability to detect joint motion. Other contexts in which spindles have also been found sufficient for proprioception in the absence of other proprioceptors include following total hip replacement surgery (Grigg et al. 1973), and following dorsal column transection at the thoracic level that greatly decreased skin and joint sensation in the legs (Wall and Noordenbos 1977).

1.1.3 ‘Active’ versus ‘Passive’ Proprioception

The sensitivity of our perceived limb position to changes in actual limb position is referred to as proprioceptive acuity. It has long been hypothesized that proprioceptive acuity is higher during ‘active’ movements (i.e., those which are self-generated) than ‘passive’ movements (i.e., those which are externally generated). The theoretical foundation for this prediction is rooted in the distinction that self-generated (‘active’) movements involve voluntary muscle contraction and externally generated (‘passive’) movements do not. The idea that acuity is higher for self-generated movements than passively guided ones is based largely on the principle of alpha-gamma coactivation (Fuentes and Bastian 2010; Gandevia et al. 1992; Laufer et al. 2001; Paillard and Brouchon 1968)—the coactivation of gamma fusimotor neurons with alpha motor neurons. That such coactivation occurs has been documented previously, and is thought to maintain the ability of the spindles to signal changes in muscle length despite losing tautness due to muscle contraction (Granit et al. 1959; Matthews 1964; McCloskey 1978; Michael-Titus et al. 2010; Vallbo 1971). That is, muscle contraction introduces slack to the intrafusal fibers, reducing the sensitivity of the spindle afferents to changes in muscle length; however, stimulation of the intrafusal fibers by gamma fusimotor nerve fibers causes them to become taut again, increasing their resting firing rate and preserving their sensitivity (see section 1.1.2). Because alpha-gamma coactivation occurs with voluntary but not passively guided movement, voluntary contraction is thought to result in an increase in spindle discharge relative to during passive movement. This may subsequently improve proprioceptive acuity relative to when movement is passively guided, by way of ameliorating the impact of slack being introduced to the intrafusal fibers during muscle contraction. It has also been proposed that a central estimate of limb position can be formed based on the corollary discharge that occurs with active muscle contraction, and that the use of such an estimate in combination with available sensory feedback ought to provide a more accurate sense of limb position than sensory feedback alone (Miall and Wolpert 1996;

Paillard and Brouchon 1968). Several studies have investigated differences in proprioceptive acuity during/after ‘active’ or ‘passive’ movement. Most have found that ‘active’ proprioception is better than ‘passive’ proprioception (Adamovich et al. 1998; Bhanpuri et al. 2013; Fuentes and Bastian 2010; Gritsenko et al. 2007; Laufer et al. 2001; Monaco et al. 2010), although others have found no difference between the two (Capaday et al. 2013; Jones et al. 2010; Yousif et al. 2015). Comparisons of proprioceptive acuity during (or after) active or passively guided movement have thus produced mixed results.

1.2 ‘Active’ and ‘Passive’ Proprioception in Multijoint Systems

1.2.1 Multijoint Movement and Interaction Torques

Like self-generated single-joint movements, self-generated movement in multi-joint systems (e.g., the upper limb) involves motion that is driven actively by muscle contraction. However, unlike single-joint movement, movement in multi-joint systems also involves motion that is not driven by active muscle contraction and is instead driven passively by interaction torque (Hollerbach and Flash 1982). Interaction torques refer to the rotational forces that arise at one joint due to motion of limb segments about other joints (e.g., forces arise at the elbow due to active shoulder motion). Indeed, dynamical interactions between segments of multijoint limbs substantially complicate movement, and skilled action often requires planning for interaction torques (Gribble and Ostry 1999; Shadmehr 2004). The development and maintenance of such plans rely on proprioception. Patients with impaired proprioception have been found to make large movement errors that vary systematically with the magnitude of interaction torques (Sainburg et al. 1993) and cannot be wholly compensated for using visual feedback (Ghez and Sainburg 1995; Sainburg et al. 1995) indicating that proprioception plays a critical role in the control of intersegmental dynamics.

1.2.2 Limb Position Sense and Torques at the Level of a Joint

Previous studies have investigated potential differences in proprioceptive acuity during active (self-generated) and passive (externally generated) limb motion. In studies where active proprioception was found to be more accurate than passive proprioception, the authors have cited the differential presence of alpha-gamma coactivation and corollary discharge as potential explanations for their findings. An interesting question is whether there might be differences in proprioceptive acuity during motion that is self-generated but not driven by active muscle contraction—that is, whether proprioceptive acuity at a particular joint might be different for joint motion driven by active muscle torque than for joint motion that is passively driven by interaction torque. If proprioceptive acuity is chiefly determined by the sensitivity of the spindles, and the sensitivity of the spindles is modulated by alpha-gamma coactivation, then acuity ought to be higher during active motion than during passive motion. One would think, then, that humans might have relatively poor acuity at joints that are moved passively by interaction torques. But during motion that involves high interaction torques, healthy humans' sense of limb position is still accurate enough to prevent the profound coordination deficits seen in deafferented patients during upper limb movement (Sainburg et al. 1993, 1995). This raises the question of whether acuity at a joint is preserved during interaction torque-driven motion despite the reduction in alpha-gamma coactivation. To address this question, we designed an experiment to determine whether limb position sense during rotation about a joint differs depending on the nature of the torques driving joint motion.

1.3 Present study

The present study sought to explore whether the nature of the torques driving joint motion influences the acuity of limb position sense at that joint. In the context of this study, proprioceptive acuity refers to the sensitivity of consciously perceived changes in limb position to actual changes in limb position. We tested proprioceptive acuity at the elbow joint while participants were midway through each of two kinds of arm movements that both involved elbow extension: one in which elbow extension was primarily driven passively by interaction torques, and one in which elbow extension was primarily driven actively by muscle torques. The two movements, termed ‘*reaching’* and ‘*whipping’* respectively, were designed to be identical in terms of the direction of elbow rotation, total distance reached, and reach duration. Differences in the magnitude and direction of shoulder rotation give rise to differences in interaction torques between ‘*whipping*’ (low interaction torques) and ‘*reaching*’ (high interaction torques) movements. With negligible interaction torques to drive displacement at the elbow, elbow extension during ‘*whipping*’ movements was produced primarily by active muscle torque. Conversely, there was minimal active muscle torque at the elbow joint during ‘*reaching*’ movements. We delivered equally sized and timed perturbations to the elbow joint during ‘*reaching*’ and ‘*whipping*’ movements and had participants make two-alternative forced choice judgements about the direction in which they were perturbed. In doing so, we were able to determine whether participants’ ability to correctly sense the direction of an elbow-joint perturbation differed depending on if the perturbation was delivered during interaction torque-driven motion or active muscle torque-driven motion. Due to differences in alpha-gamma coactivation between the two types of movement, we hypothesized that proprioceptive acuity would be higher during active muscle torque-driven motion than during motion that was driven by interaction torques.

Chapter 2

2 Methods and Materials

2.1 Participants

A total of 15 healthy individuals (9 female) participated in this study over single sessions lasting approximately two hours. Participants' ages ranged from 18-20 (mean 18.4 years). All participants were students at Western University who reported being right-handed and reported normal or corrected-to-normal vision (glasses or contacts were permitted). No participants reported having any neurological, visual, or musculoskeletal disorders. Informed, written consent was obtained from all participants prior to their participation in the study. Participants received financial compensation and/or course credit in exchange for their time. This study was approved by the Western Research Ethics Board.

2.2 Apparatus

Participants completed this experiment using a robotic exoskeleton (KINARM, Kingston, ON, Canada). The exoskeleton allowed participants to perform horizontal planar arm reaching movements and was capable of independently applying torques at the shoulder or elbow joints. The exoskeleton's link lengths were adjusted to fit each participant, and the robot was calibrated such that a small white cursor was colocalized with the tip of each participant's right index finger, providing a visual marker of hand position—the visibility of which could be experimentally manipulated (visible or not visible) during the session. Throughout this experiment, participants reached to visual targets that were projected onto a horizontally-mounted display, which was located above the limb's workspace, below eye level. Direct vision of the arm was occluded by the opaque display and an additional opaque draping that originated from the edge of the display and was secured around the back of the participant’s neck.

2.3 Experimental Design

2.3.1 Summary

In a single testing session, every participant completed two experimental blocks (*‘whipping’* or *’reaching’*) that each involved performing one of two types of planar arm reaching movements (*‘whipping’* or *‘reaching’*) with the right arm. The two movements differed in terms of the direction in which participants were instructed to reach—which, in turn, gave rise to differences in interaction torques at the elbow joint. During experimental blocks, participants occasionally received a brief elbow-joint perturbation in the middle of their reach, which induced a transient flexion or extension of varying magnitude at the elbow. Participants were then asked to report on whether they felt that their elbow had been perturbed into flexion or extension. Each experimental block was immediately preceded by a training block in which participants practiced reaching in the same direction as the corresponding experimental block, were familiarized with the perturbations, and were screened to ensure they could distinguish between flexion and extension when the perturbation size was very large. The order in which participants completed the two experimental blocks (and their corresponding training blocks) was counterbalanced across participants, with 7 of the 15 participants having completed the *‘whipping’* condition (training + experimental) first. We used participants’ binary responses across varying magnitudes of flexion and extension to determine proprioceptive acuity at the elbow joint during ‘*whipping’* or *‘reaching’* movements.

2.3.2 Selection of ‘Reaching’ and ‘Whipping’ Trajectories

Depending on the direction of an arm reaching movement, extension of the elbow can be driven mostly by passive interaction torque, mostly by active muscle torque, or by a combination of both. For example, when reaching to an end-point in the periphery of the contralateral field (a *‘reaching’* movement), motion at the elbow joint is driven mostly by passive interaction torque, but when reaching to an end-point in the periphery of the ipsilateral field (a *‘whipping’* movement), elbow joint motion is driven mostly by active muscle torque (Hollerbach and Flash 1982).

In this experiment, we wanted to manipulate the extent to which elbow joint motion was driven by interaction torque or active muscle torque. Specifically, we wanted participants to perform one movement (*‘reaching’*) in which elbow motion involved high interaction torque and low muscle torque, and another movement (*‘whipping’*) in which elbow motion involved low interaction torque and high muscle torque. To determine the reach angles that would maximize (for the *‘whipping’* movement) or minimize (for the *‘reaching’* movement) muscle torque at the elbow joint during planar reaching movements, we simulated minimum-jerk hand trajectories (Hollerbach and Flash 1982) for 64 different reach angles and then computed, using inverse dynamics, the muscle torque that would need to be applied at the shoulder and elbow to generate those movements (Gribble and Ostry 1999). Where there was elbow extension but minimal muscle torque applied at the elbow during the reach, we reasoned that the extension must have been driven by interaction torque. To choose angles for our *‘reaching’* and *‘whipping’* movements, we selected the angles which produced the minimum or maximum muscle torque at the elbow in our simulation (rectified and integrated over the duration of the reach). The reaches we simulated were 24 cm in length and ~1 second in duration. We chose these values because we had experimentally determined this reach distance and duration to be the most compatible with the position-control system that we used for generating perturbations. Simulated reaches also satisfied a requirement for the elbow and shoulder angles to approach 90 and 45 deg respectively at the midpoint of the reach. We set these criteria to ensure that the joint angles at the time of the perturbation would be similar for *‘whipping’* and *‘reaching’* movements. From our simulations, we found that muscle torque at the elbow was highest for a reach angle of 46 deg and lowest for a reach angle of 132 deg (Figure 1). Conversion of the start and end hand positions for these two trajectories to joint coordinates, based on general assumptions about link length and mass, gave start and end shoulder and elbow coordinates of (24.3, 108.4) deg and (65.9, 65.8) deg for the *‘reaching’* movement, and (47.6, 102.7) deg and (47.9, 71.8) deg for the *‘whipping’* movement (Figure 2A, B). We verified empirically—using inverse dynamics computations that were based on KINARM dynamics (KINARM, Kingston, ON, Canada), kinematic data obtained during our experiment, and subject-specific inertial parameters (Winter 1990)—that the angles we selected resulted in higher muscle torque being produced for the *‘whipping’* movement than the *‘reaching’* movement (Figure 2C).

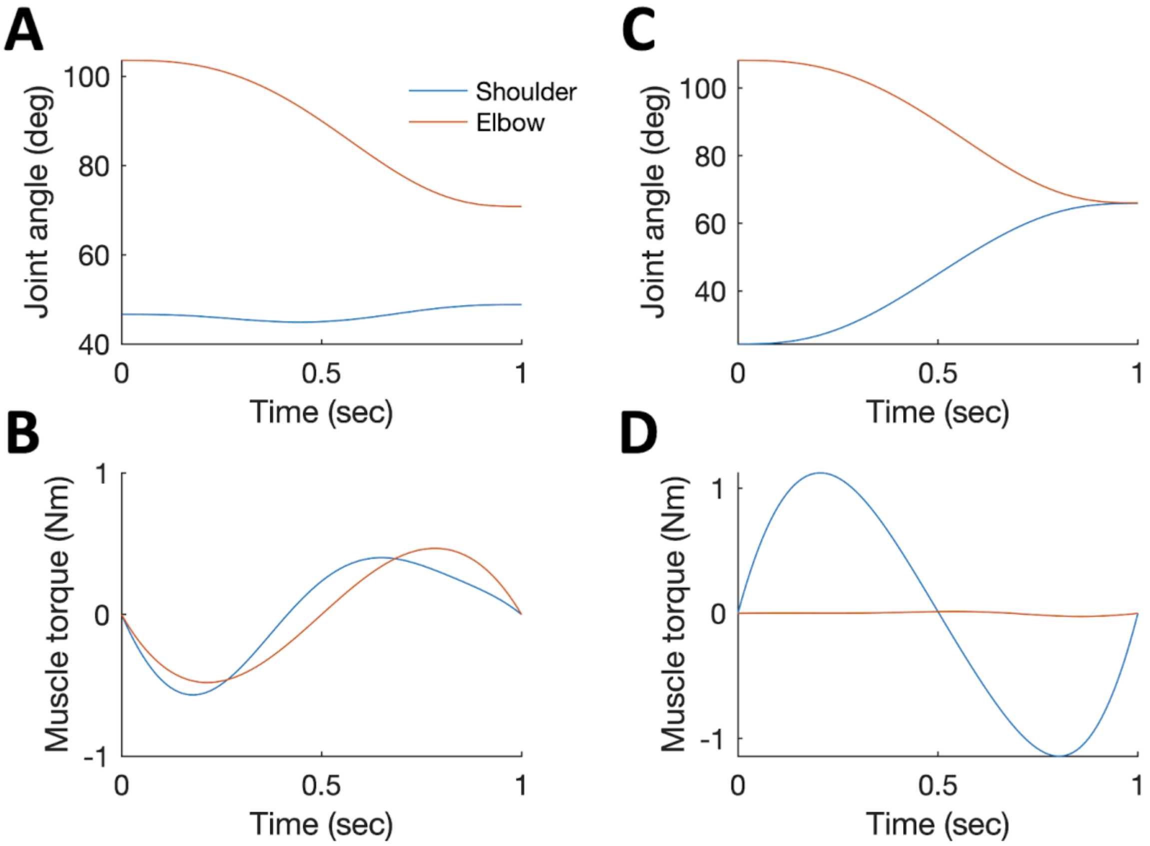

Figure 1. Simulated joint angles ***(A)*** and muscle torques ***(B)*** at the shoulder and elbow over the time course of a 1-second reach performed on a 46-degree angle; simulated joint angles ***(C)*** and muscle torques ***(D)*** at the shoulder and elbow over the time course of a 1-second reach performed on a 132-degree angle. The former reach was selected as our *'whipping'* movement, and the latter was selected as our *'reaching'* movement.

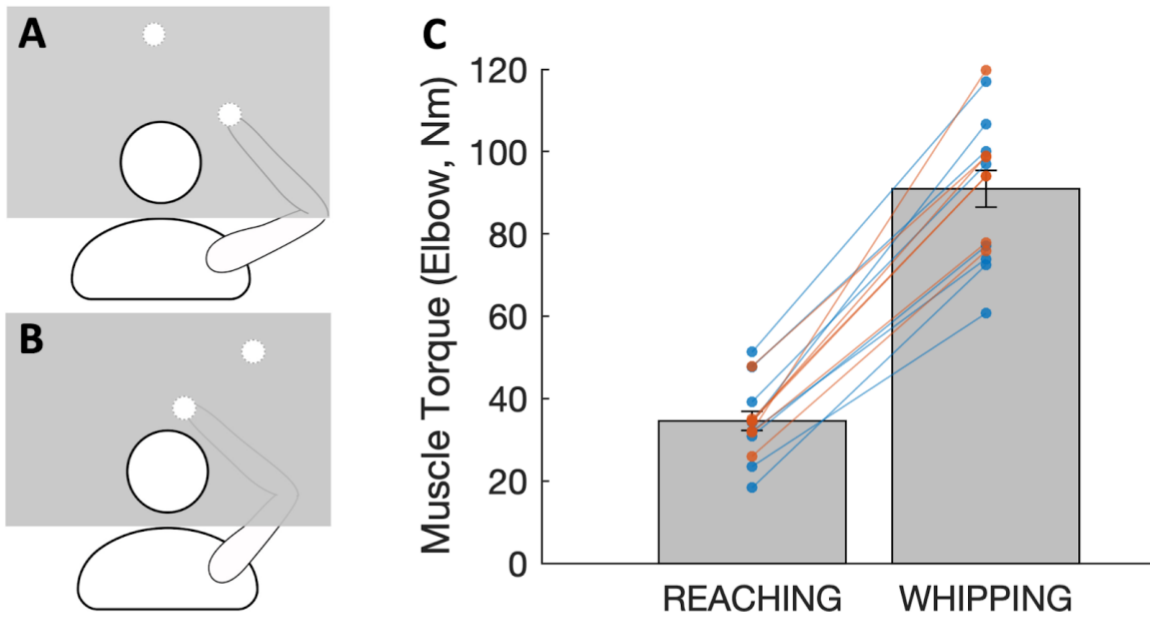

Figure 2. Schematic representation of starting limb configuration, and start- and end-targets, for ***A.*** *'reaching'*, and ***B.*** *'whipping'* movements. ***C.*** Mean (± SE) integrated rectified muscle torque at the elbow across all (N=283 trials/participant) non-perturbation trials in the *'reaching'* or *'whipping'* experimental blocks. Muscle torque was computed using inverse dynamics and subject-specific inertial parameters, then rectified and integrated from the time participants left the start-target to the time they entered the end-target. Individual subject means are plotted in blue for those who completed the *'reaching'* condition first, or orange for those who completed the *'whipping'* condition first. Muscle torque at the elbow was significantly higher for *'whipping'* than *'reaching'* movements ($t(14)=-17.04$, $P<0.001$).

2.3.3 Task

For each condition (*‘reaching’* or *‘whipping’*), participants underwent a training block and an experimental block. Except for the location of the start- and end-targets, the training and experimental blocks were the same for both conditions. Each condition contained only one start-target and one end-target. Visually, each target was shown as an open circle with a 1 cm radius and a white outline. Upon arriving at a target, the feedback cursor that represented the tip of the index finger filled the open circle.

2.3.3.1 General task parameters

Throughout this experiment participants performed point-to-point reaches with the right arm. They were instructed to wait in the start-target until the end-target appeared on the screen (500 ms later), then reach to the end-target in a straight line. Upon entering the end-target, the robot initiated a passive return of the hand back to the start-target. Participants were also instructed to try to reach the end-target in approximately 1 second. If the end-target was reached within 950–1150 ms of leaving the start-target, the end-target turned green upon entry. Otherwise, it turned blue (too slow) or red (too fast). Trials were not excluded on the basis of the reach time; the colour feedback was only intended to help participants regulate their speed. With the exception of the first 30 reaches in either training block (during which the cursor was always visible), the cursor that represented the location of the hand was only visible when the tip of the index finger was within 1.5 cm of the start- or end-target. That is, the cursor was removed shortly after leaving the start-target and only returned when approaching the end-target, so that participants received no visual feedback about hand position during the majority reach (including during the perturbation).

2.3.3.2 Training blocks

The training block consisted of four stages: practice reaches (with cursor), practice reaches (with disappearing cursor), familiarization with sample perturbations, and quiz.

Participants first performed 30 practice reaches with their cursor visible at all times, then performed 40 practice reaches where the cursor disappeared during the reach, as described in section 2.3.3.1. Following the completion of these practice reaches, participants were told that the robot would now “gently nudge” them occasionally, in the middle of their reach. They were told that the robot would transiently nudge their elbow “towards” or “away from” their body prior to returning them back to their original trajectory. The experimenter, by raising their own arm to the approximate configuration of the participant’s, demonstrated “towards” as a bending of the elbow, and “away” as an extension of the elbow. Participants were instructed to identify the former as “flexion” and the latter as “extension”. Prior to resuming reaching, participants were asked to demonstrate what flexion and extension look like by moving their arm while still placed in the exoskeleton. All participants did so successfully. Participants were also instructed to not intervene in the event that they should receive a perturbation. Specifically, they were asked to try not to “clench” or resist the perturbation, and told that they should simply relax, proceed with their reach as usual, and “let the robot nudge [them]” because it would bring them back to their original trajectories right after the initial displacement. This is to say, we communicated that any perturbations would be gentle, transient, and not influence performance; and we specifically instructed participants to stay relaxed and to proceed as if no perturbation had occurred.

Participants then resumed reaching and were given 5 flexion perturbations in ratios of 3 unperturbed to 1 perturbed reach (in that order), followed by 5 extension perturbations in the same 3:1 ratio. These perturbations were larger than the largest of those delivered during experimental blocks (see ‘servo-controlled position perturbations’ below). After exposure to the sample perturbations, participants were instructed that they would now be ‘quizzed’ on their ability to distinguish flexion from extension. They completed 50 reaches, of which 10 were perturbation trials (5 flexion and 5 extension). The perturbations were delivered in pseudorandom order, such that perturbation trials were separated by no less than two unperturbed trials. Upon entering the end-target after receiving a perturbation, participants made a two-alternative forced choice judgment about whether they felt they had been perturbed into flexion or extension. The robot initiated a passive return to the start-target once the participants’ responses were recorded by the researcher. All participants achieved 100% accuracy on the quiz before moving on to the experimental block.

2.3.3.3 Experimental blocks

Participants entered the experimental block following completion of its corresponding training block. The experimental block began with 35 unperturbed reaches, followed by 320 reaches that included 64 perturbation trials and 8 ‘sham’ perturbation trials, on which no perturbation occurred but participants were still required to report whether they felt flexion or extension. The perturbations were pseudorandomly interspersed, such that perturbation trials were separated by no less than two unperturbed trials. Following each perturbation trial (including shams), participants made a two-alternative forced choice judgment about whether they had been perturbed into flexion or extension, and were passively returned back to the start-target once their response had been recorded. Details about the perturbations are presented below.

2.3.3.4 Servo-controlled position perturbations

We used a servo controller to deliver position perturbations at the elbow joint during reaching. In summary, during a given perturbation trial, our controller compared the current elbow velocity profile to those of the last 30 unperturbed reaches, then used the closest match to predict the future trajectory of the elbow angle on the current trial if the elbow were not perturbed. The controller then perturbed the forearm to cause a transient deviation of the elbow angle from the predicted trajectory by some commanded number (0.5, 1, 1.5, or 2) of degrees in either direction (flexion or extension) and immediately returned the elbow back to its original angular trajectory. The total duration of the perturbation was 400 ms. Each experimental block contained 8 perturbations of each commanded magnitude-direction combination (e.g., eight of the 64 non-sham perturbations in an experimental block were commanded to be 1 deg flexions). The perturbations in the training blocks were all commanded to be 3 deg in magnitude.

The controller was developed according to the method described in Burdet *et al.* (2000), with some modifications. Rather than storing velocity profiles from the last 10 unperturbed reaches, our controller stored velocity profiles from the last 30 unperturbed reaches. We also did not average or scale the stored velocity profiles to generate candidate profiles. Instead, candidate profiles were simply selected from the 30 that had been stored. Lastly, we did not screen new velocity profiles prior to storing them; the velocity profile of each new unperturbed trial always displaced the oldest of the 30 stored.

2.4 Analyses

2.4.1 Kinematic Recordings and Analyses

Hand positions and joint angles were digitally sampled at 1000 Hz during participants’ movements, then low-pass filtered (15 Hz, double-pass, third-order Butterworth filter). Kinematic data from individual trials were aligned on the time at which 30% of the total reach distance had been completed. Perturbations were initiated at the time at which 30% of the reach distance was completed on the candidate trial whose velocity profile was selected by the controller as the best match to the current perturbation trial. Since the velocity profile for the current trial was similar to the matched profile, the true time of perturbation onset closely corresponded (± 50 ms) with the time at which 30% of the reach distance was completed on the current trial. We designated the latter time point the 'trigger time'. While we could have aligned perturbation trials on the recorded perturbation onset time, we could not have done so for non-perturbation trials, since they lacked true perturbation onset times. Instead, the time at which 30% of the reach distance was completed (i.e., the trigger time) was used for aligning kinematic data from all trials.

All joint angles reported here refer to external joint angles (Figure 3A). Accordingly, the sign convention for flexion is positive, and the sign convention for extension is negative. Trajectories from a sample unperturbed trial, a sample flexion perturbation trial, and a sample extension perturbation trial are shown in Figure 3B.

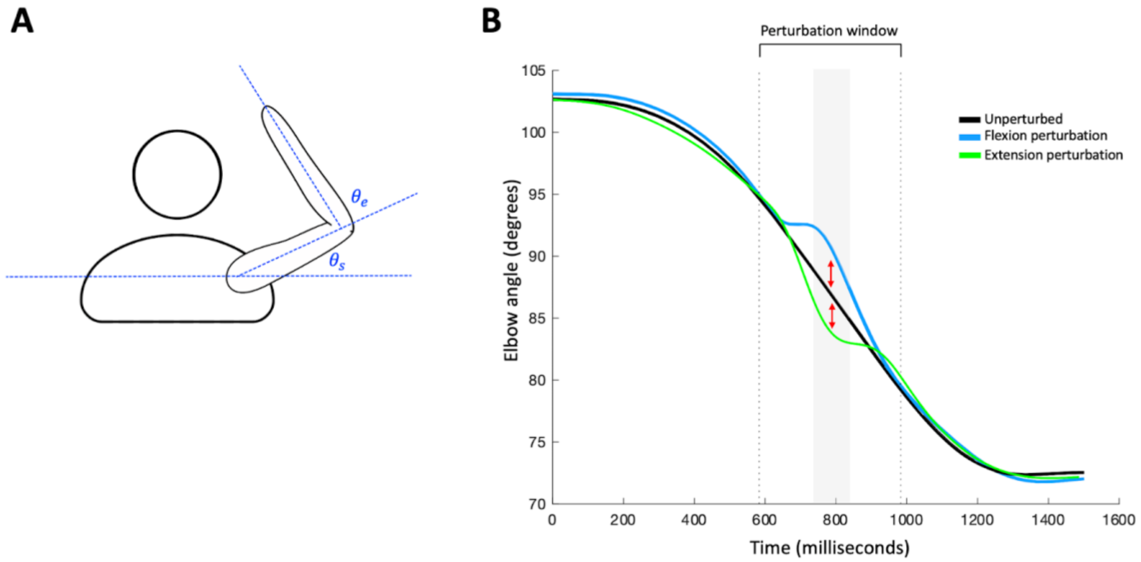

Figure 3. ***A.*** Joint angle conventions. ***B.*** Sample elbow angle trajectories for an unperturbed trial (black), flexion perturbation (blue), or extension perturbation (green).

2.4.2 Empirical Determination of Perturbation Size

Ideally, the magnitude of a perturbation would have been quantifiable by computing the difference between the actual, perturbed elbow angle and the controller's prediction of what the elbow angle would have been if no perturbation had occurred. However, the controller we used to generate perturbations often made poor predictions of the unperturbed elbow angle. While these predictions were usually sufficient to generate a transient perturbation in the commanded direction with an almost seamless return back to the original trajectory, their use in quantifying the amount of flexion or extension experienced during a perturbation produced inaccurate measurements of perturbation size. In place of the controller's predicted elbow trajectories, we generated new, velocity-based predictions of unperturbed elbow trajectory, which we then used to empirically determine the magnitude of the perturbations we delivered. The procedure used to predict unperturbed trajectories is described below. Perturbation magnitude was quantified as the maximum difference between the actual, perturbed elbow angle and the predicted unperturbed elbow angle (according to our velocity-based prediction) within the middle 100 ms of the perturbation (Figure 3B).

2.4.2.1 Predictions of unperturbed elbow trajectory

We considered two possible methods for predicting unperturbed elbow angle trajectories on perturbation trials: position matching or velocity matching. To determine which method more reliably predicted unperturbed trajectories, we generated position- or velocity-based predictions for non-perturbation trials and compared the actual trajectories to those predicted.

Position- or velocity-based predictions of unperturbed elbow angle were generated by first selecting, from the last 50 unperturbed reaches, the trial for which elbow position or velocity most closely matched the current trial. Position-based matching involved computing the sum of squared errors (SSE) between the elbow angle on the current trial and the angle on each candidate trial, over a 550 ms period ending 50 ms before the trigger time. The best match was that with the lowest SSE, and the position data from the selected trial formed the position-based prediction of the unperturbed trajectory on the current trial. Velocity-based matching involved computing the SSE between elbow velocity on the current trial and velocity on each candidate trial, over the same 550 ms period. The best match was that with the lowest SSE, and the position data from the selected trial formed the velocity-based prediction of the unperturbed elbow trajectory on the current trial.

For each participant, we tested the fits of the position- or velocity-based predictions to the actual data from all but the first 50 non-perturbation trials in each experimental block (474 total test trials per participant). For each trial tested, the superiority of one prediction over the other was established by computing, for each of the two predictions, the SSE between the predicted and actual elbow trajectories in the 400 ms following the trigger time (i.e., the equivalent of the perturbation window). The prediction with the lower SSE was deemed superior. For any individual participant, the velocity-based prediction was superior or equal to the position-based prediction on >60% (*M* = 68.83%, *SD* = 2.85%) of trials. We concluded that the velocity-based prediction fit the real unperturbed trajectory as well as or better than the position-based prediction the majority of the time.

To verify that our velocity-based predictions provided equal or better estimates of unperturbed elbow trajectory than the servo controller's predictions, we repeated the above procedure for sham perturbation trials. Since participants were not perturbed on sham trials, for every such trial (16 per participant) we computed the SSE between the predicted and actual trajectories within the perturbation window (Figure 4). On $\geq$50% (*M* = 69.17% *SD* = 9.59%) of sham trials completed by any individual participant, the SSE between our velocity-based prediction and the actual trajectory (SSE_v) was less than or equal to the SSE between the controller's prediction and the actual trajectory (SSE_c). Importantly, the controller's predictions were sometimes extremely erroneous. The mean SSE_c was over 5 times higher than the average SSE_v (median > 4 times higher). For 15.42% of the controller's predictions, the SSE_c was higher than the maximum SSE_v given by any velocity-based prediction, and the maximum SSE_c exceeded the maximum SSE_v by 22.7 times. We concluded that our velocity-based predictions provided more reliable estimates of the unperturbed trajectory than did the servo controller's predictions.

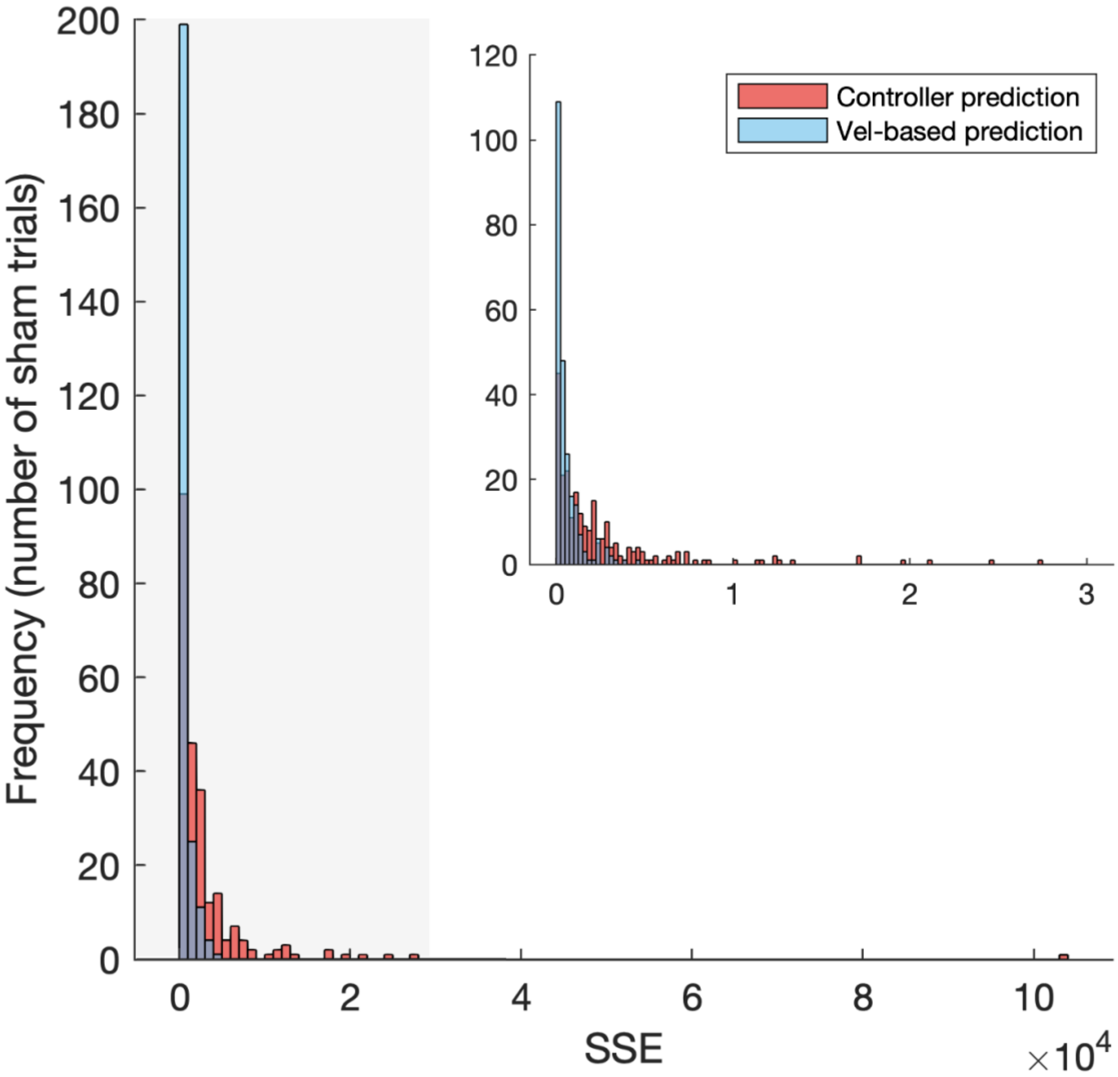

Figure 4. Sum of Squared Errors (SSE) between the predicted and actual elbow angle trajectories on sham trials (N=240 trials across 15 participants). SSE between the position controller's prediction or the velocity-based prediction and the actual trajectory was computed across the 400 ms following the trigger time. **Inset:** Finer-grained view of the data from within the grey box.

2.4.3 Exclusion of Perturbation Trials

As noted above, the servo controller's predictions about the unperturbed elbow trajectory could at times be quite flawed. Since the controller was programmed to cause a predetermined amount of flexion or extension of the elbow relative to the predicted angular trajectory, if the controller’s prediction was inappropriate, the perturbation was sometimes also inappropriate. Some examples are outlined here.

Consider a situation in which the controller’s predicted trajectory was shifted such that the predicted elbow angle was too large during the perturbation window (i.e., on the participant’s natural, unperturbed trajectory, the elbow would be in a state of extension relative to the controller’s prediction). On such a trial, an attempt by the controller to cause an *n*-deg extension of the elbow would actually cause elbow flexion if *n* were less than the magnitude of the error between the true unperturbed trajectory and the controller’s prediction. This is because, to carry out the perturbation, the controller would bring the forearm to a position at which the elbow angle is negative *n*-deg away from the predicted angular trajectory—which, in this case, is some positive number of degrees away from the angular trajectory the elbow was really headed for. Situations like this were problematic when they happened in practice, not only because the direction of the perturbation was opposite that commanded, but also because this tended to distort the shape and smoothness of the perturbation. However, not all trials on which the controller’s prediction erred on the side opposite the commanded perturbation direction were problematic. For example, if in the above-described situation *n* were to exceed the magnitude of the error between the true unperturbed trajectory and the controller’s prediction, then an attempt by the controller to cause an *n*-deg extension would still cause elbow extension, just to a lesser degree than was commanded. When such circumstances occurred in practice, as long as *n* was sufficiently larger than the prediction error and the predicted elbow angle fell within the range of the participant’s natural reach variability, the perturbation was generally not distorted and still involved a smooth deviation and return of the elbow to its original trajectory. If these conditions were not satisfied, the controller’s attempt to ‘return’ the elbow angle to the erroneous, predicted trajectory following the small initial perturbation often resulted in a clear overshooting of the participant’s forearm relative to where it would reasonably have been if no perturbation had occurred. This effectively perturbed the elbow in the wrong direction and did so in a manner that lacked the transience of a normal perturbation. Despite this, it is again worth noting that not all trials for which the controller’s prediction was erroneous were problematic. For example, situations where the controller’s prediction erred on the same side as the commanded direction of the perturbation rarely posed an issue, since this tended to result in the elbow being perturbed in the correct direction, just to a greater extent than intended.

We restricted our analyses to include data from only those perturbation trials for which the elbow was perturbed in the intended direction via a smooth and appropriately shaped bump. Trials that met these criteria were identified by manual classification. For every individual perturbation trial, we visually inspected plots that overlaid the actual perturbed trajectory with three different predictions of the unperturbed trajectory: the controller’s prediction, the velocity-based prediction (computed as described in section 2.4.2.1), and the average trajectory of the 10 non-perturbation trials that preceded the perturbation trial being assessed. Trials were excluded if during the perturbation window the perturbed trajectory deviated from both the average and velocity-based trajectories in the opposite direction than intended (as described above). We also inspected the commanded elbow torque profile for each trial to verify that the direction of torque applied to the elbow to generate the perturbation matched the intended perturbation direction (e.g., torques should have been applied in the direction of elbow flexion if the trial was supposed to be a flexion perturbation). Trials were excluded if there was disagreement between the direction of the commanded elbow torque and the intended direction of the perturbation, which reflected an attempt by the controller to perturb the elbow in the wrong direction, either from the beginning of the perturbation or on the return back to the unperturbed trajectory. Manual classification was completed without knowledge of whether participants reported being perturbed into flexion or extension on any trial.

2.4.4 Analysis of Proprioceptive Data

For each participant, a psychometric curve for each experimental condition (*‘whipping’*, *‘reaching’*) was generated using the two-alternative forced choice responses recorded across all perturbation trials that were classified as eligible for inclusion. Participants’ binary responses (“flexion” or “extension”) were plotted against empirically determined perturbation size. Psychometric functions relating the perceived perturbation direction to the perturbation size were estimated by fitting the binary response data across various perturbation sizes to a binomial model using a cumulative normal distribution function. A sample psychometric curve generated using a single participant’s data from one experimental condition is shown in Figure 5.

The distance spanning the 25th and 75th percentiles of the psychometric function is often referred to as uncertainty range (UR), a measure that is inversely related to proprioceptive acuity (Henriques & Soechting, 2003). Within subjects, we compared the URs computed for *‘reaching’* and *‘whipping’* movements to determine whether proprioceptive acuity at the elbow joint differed between the two types of motion. The statistical test we performed for this comparison was a paired-samples *t*-test. Statistical tests were completed in Matlab R2021b.

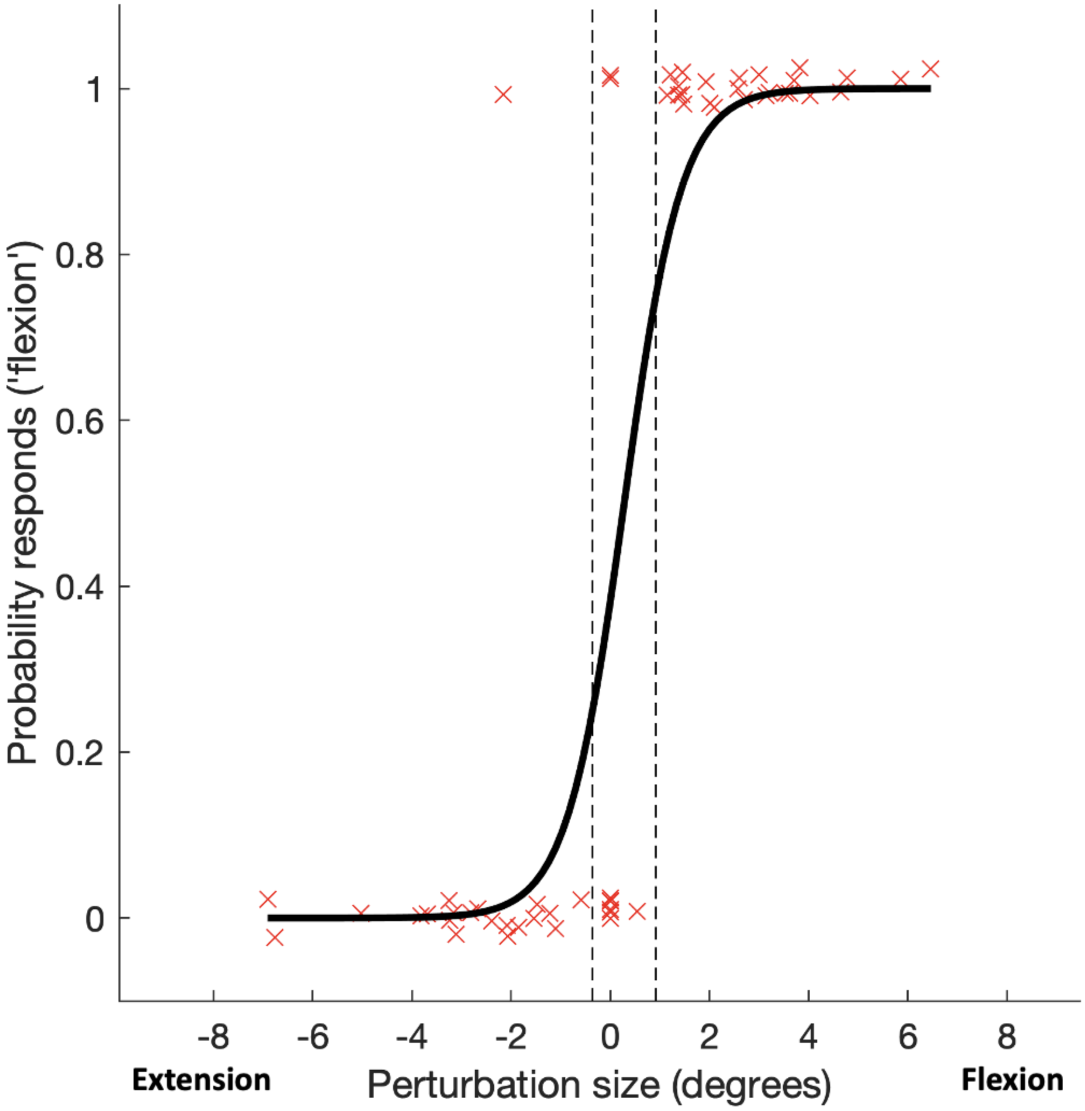

Figure 5. Sample psychometric curve from one experimental block for a single participant. Two-alternative forced choice responses (“flexion” or “extension”) are plotted against empirically determined perturbation size. The probability that the participant responded “flexion” for a given perturbation size is modeled by the psychometric function. The 25th and 75th percentiles are marked by dotted vertical lines. The Uncertainty Range (UR) was computed as the distance (in degrees) between the vertical lines.

2.4.5 Analyses Related to Angular Elbow Speed

As discussed in section 2.3.2, we designed our *'reaching'* and *'whipping'* trajectories such that the cartesian distance spanned by the hand, and the duration of the reach, would be approximately the same for both trajectories. We did not design them to hold the amount of rotation that occurred at the elbow joint constant between *'reaching'* and *'whipping'* movements. As a result, the start and end shoulder and elbow coordinates were (47.6, 102.7) deg and (47.9, 71.8) deg for the *'whipping'* movement, and (24.3, 108.4) deg and (65.9, 65.8) deg for the *'reaching'* movement—necessitating greater rotation about the elbow joint to complete the *'reaching'* than the *'whipping'* movement, despite the movements having common reach time constraints. We assessed empirically whether the speed of rotation about the elbow joint differed between *'reaching'* and *'whipping'* movements, by comparing participants' average angular elbow speed across all perturbation-absent *'reaching'* or *'whipping'* movements using a paired-samples *t*-test. For this analysis, the average angular elbow speed on a given perturbation-absent trial was taken across a 1500 ms time period beginning 600 ms before the trigger time (see section 2.4.1), and the resulting metric was averaged across all trials of the same type *('reaching'* or *'whipping'*) for each participant.

We then performed three sets of additional analyses to determine whether there was any relationship between angular elbow speed and proprioceptive acuity among our participants. First, for each of the '*reaching'* and *'whipping'* movements (separately), we regressed participants' URs onto their mean angular elbow speeds and computed least-squares lines of best fit. The relationship between mean angular elbow speed and UR for each type of movement ('*reaching'* or *'whipping'*) was assessed for significance by *F*-testing each model. Second, we performed another simple linear regression analysis in which the difference in participants' URs ('*reaching*' UR – '*whipping'* UR) was regressed onto the difference in their mean angular elbow speeds ('*reaching'* elbow speed – '*whipping*' elbow speed) between *'reaching'* and *'whipping'* conditions. The model was statistically assessed by *F*-test. Third, for each of the *‘reaching’* and *‘whipping’* conditions, we split participants into tertiles based on their mean angular elbow speeds and compared—by two-sample *t*-test—the URs of participants in the bottom speed tertile to the URs of participants in the top speed tertile.

All analyses were carried out in Matlab R2021b.

Chapter 3

3 Results

3.1 Uncertainty Ranges

Within-subjects, we compared the uncertainty range (UR) obtained from *'reaching'* and *'whipping'* conditions to determine whether proprioceptive acuity at the elbow joint differed between the two types of motion. We found that participants' UR was significantly smaller for '*reaching'* movements than for '*whipping'* movements (*t*(14)=-2.3267, *P*=0.0355; Figure 6). There is one potential outlier included in this dataset; however, removing that participant's data from the analysis did not change the result. Without the potential outlier, participants' UR was still significantly smaller for '*reaching'* movements than '*whipping'* movements (*t*(13)=-2.3300, *P*=0.0366).

3.2 Angular Elbow Speed

To select trajectories for the *'whipping'* and *'reaching'* movements, we simulated hand trajectories in cartesian space and converted the start and end hand positions for the selected trajectories to joint coordinates based on general assumptions of link length. This resulted in the *'reaching'* movement involving a greater amount of rotation about the elbow joint than the *'whipping'* movement; however, participants were instructed to complete both movements in the same time frame. The average speed of elbow rotation was higher for the *'reaching'* than the *'whipping'* movement (*t*(14)=-71.03, *P*<0.001; Figure 7).

To determine whether there was a relationship between angular elbow speed and proprioceptive acuity among our participants, we performed simple linear regression of participants' URs onto their average angular elbow speed within a given condition ('*reaching'* or '*whipping*'). For both *'reaching'* and *'whipping'* conditions, we found that average angular elbow speed did not explain a significant amount of the variance in UR (*‘reaching’*: R^2 = 0.018, *F*(1,13)=0.24, *P*=0.63; *‘whipping’*: R^2=0.149, *F*(1,13)=2.27, *P*=0.16; Figure 8A, B). Additionally, change in average angular elbow speed between *‘reaching’* and *‘whipping’* conditions did not predict change in UR between *‘reaching’* and *‘whipping’* conditions (R^2=0.0497, *F*(1,13)=0.68, *P*=0.43; Figure 8C). Finally, within a given condition (*‘reaching’* or *‘whipping’)*, we found no significant difference in UR between participants whose average angular elbow speed fell within the bottom third (*N*=5) or the top third (*N*=5) of angular elbow speeds (*‘reaching’*: *t*(8)=-0.34, *P*=0.74; *‘whipping’*: *t*(8)=1.44, *P*=0.19; Figure 9). We have therefore found no evidence of a relationship between the speed of rotation about the elbow joint, and proprioceptive acuity, in this task.

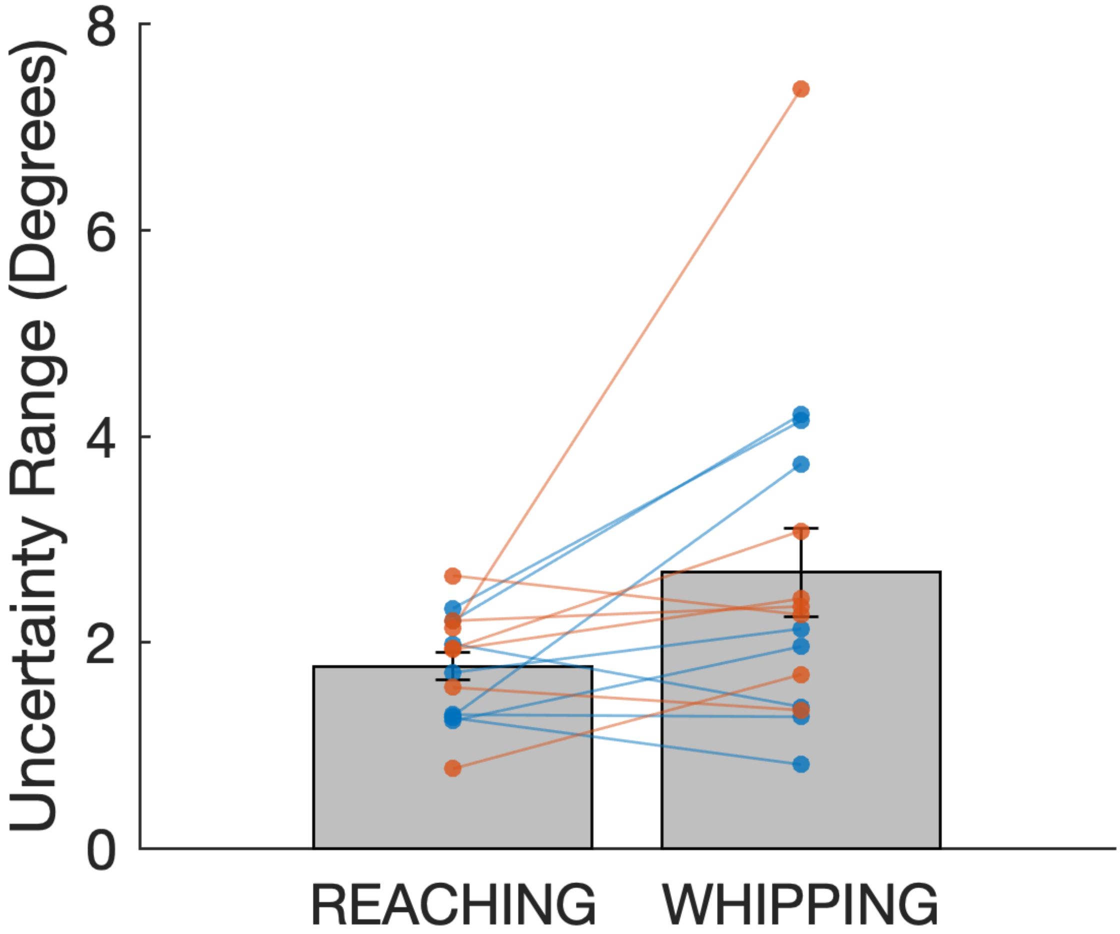

Figure 6. Mean (± SE) Uncertainty Range (UR) for the *'reaching'* and *'whipping'* experimental blocks. URs for individual subjects are plotted in blue for those who completed the *'reaching'* condition first, or orange for those who completed the *'whipping'* condition first. UR was significantly higher for the *'whipping'* condition than for the *'reaching'* (*t*(14)=-2.33, *P*<0.05).

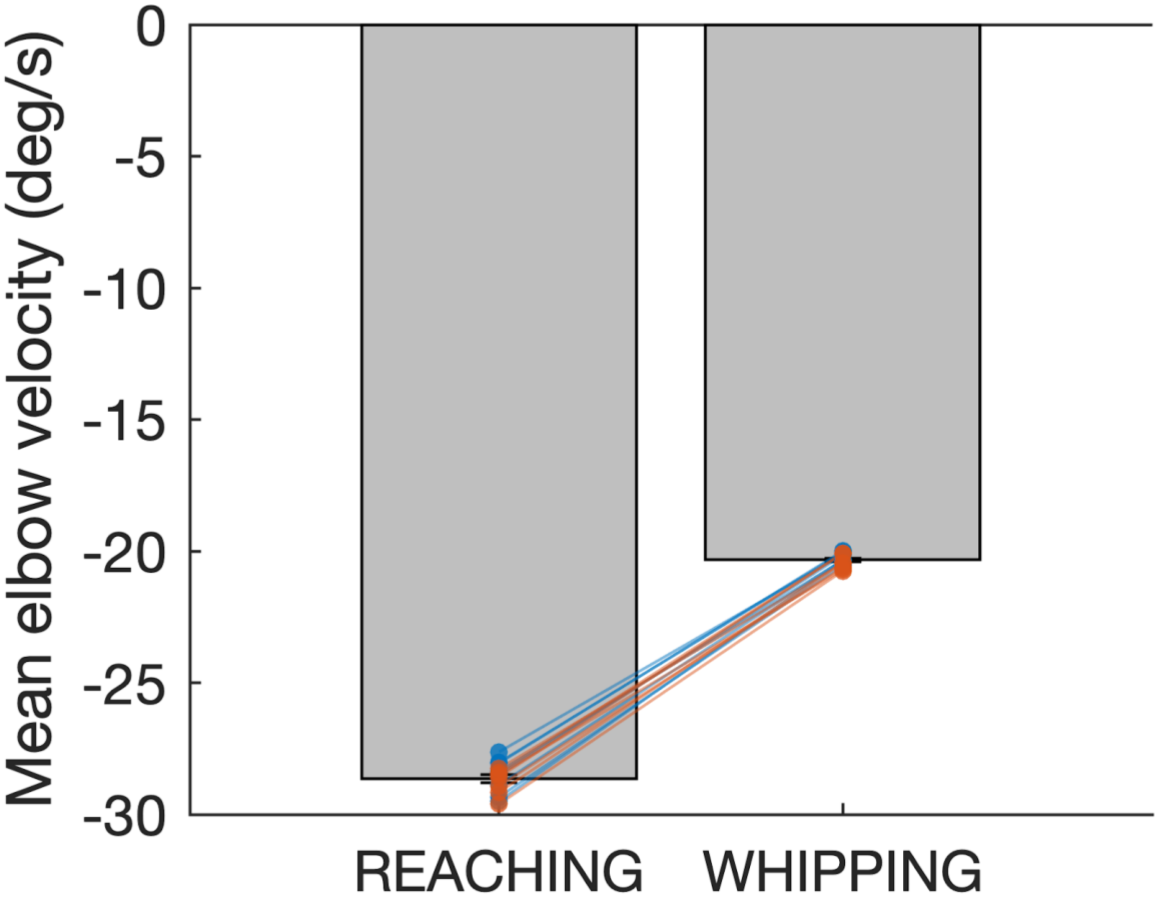

Figure 7. Average angular velocity about the elbow joint for *'reaching'* and *'whipping'* movements. Velocities for individual participants are plotted in blue for those who completed the *'reaching'* condition first, or orange for those who completed the *'whipping'* condition first. The speed (i.e., magnitude of velocity) of elbow rotation was significantly faster for *'reaching'* than *'whipping'* movements ($t(14)=-71.03$, $P<0.001$).

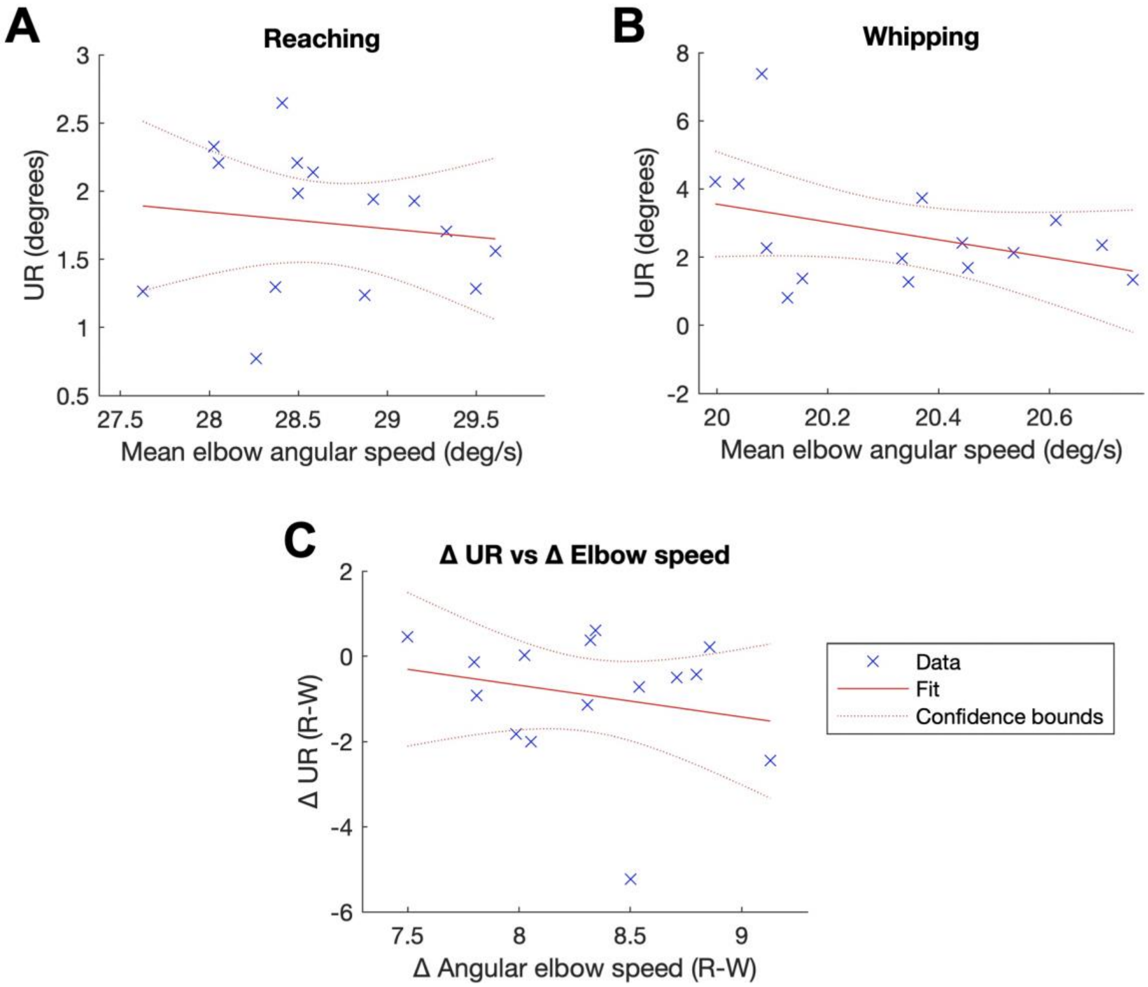

Figure 8. Uncertainty range (UR) versus mean angular elbow speed during the *'reaching'* block (**A**), and *'whipping'* block (**B**). (**C**) Within-subject differences in UR between *'reaching'* and *'whipping'* blocks versus within-subject differences in mean angular elbow speed between *'reaching'* and *'whipping'* blocks. Blue crosses represent data points from individual participants; solid red lines and dotted red boundaries reflect modeled least-squares lines of best fit and 95% confidence bounds. Mean angular elbow speed was not found to be a significant predictor of UR in *'reaching'* ($R^2 = 0.018$, $F(1,13)=0.24$, $P=0.63$) or *'whipping'* ($R^2=0.149$, $F(1,13)=2.27$, $P=0.16$) blocks. Change in mean angular elbow speed from *'whipping'* to *'reaching'* blocks was also not found to predict change in uncertainty range from *'whipping'* to *'reaching'* blocks ($R^2=0.0497$, $F(1,13)=0.68$, $P=0.43$).

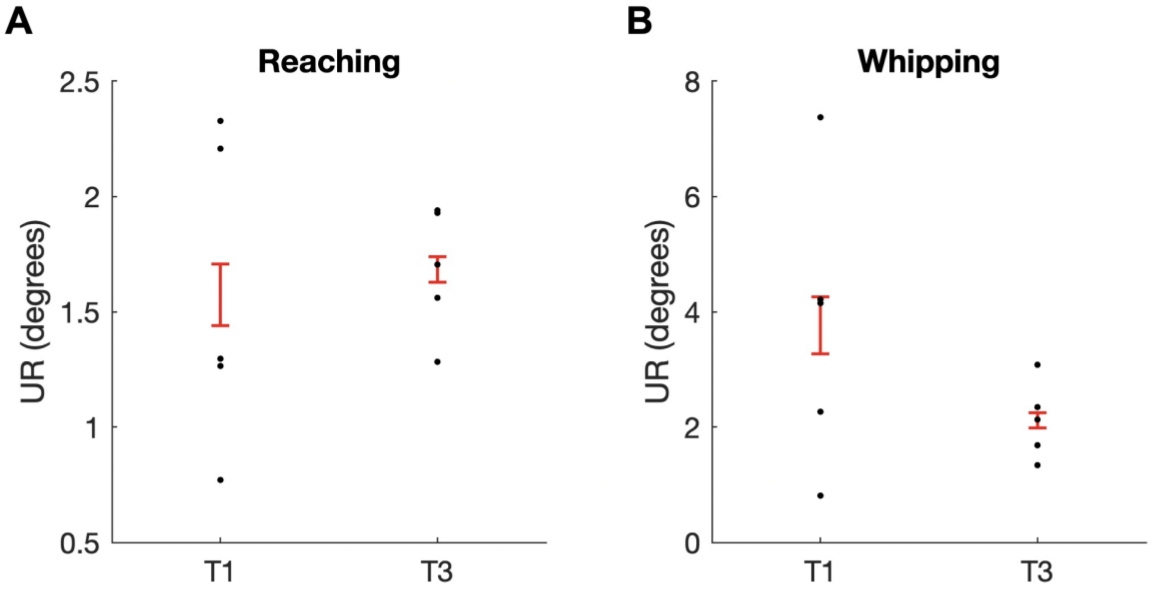

Figure 9. Uncertainty range (UR) for participants whose average angular elbow speed fell within the bottom tertile (T1) or top tertile (T3) of elbow speeds for the *'reaching'* (**A**) or *'whipping'* (**B**) movement. Red lines represent the mean UR (± SEM); black dots represent individual participant URs. For both movements, the mean UR of participants in T1 did not significantly differ from the mean UR of participants in T3 (*'reaching'*: *t*(8)=-0.34, *P*=0.74; *'whipping'*: *t*(8)=1.44, *P*=0.19).

Chapter 4

4 Discussion

Whether there are differences in proprioceptive acuity during ‘active’ and ‘passive’ motion has been explored extensively in the context of self-generated (i.e., driven by voluntary muscle contraction) and externally-generated (i.e., passively guided) movements, respectively. Although findings have been mixed, the majority of the existing literature on active and passive proprioception supports the idea that limb position sense is more accurate during self-generated movement than for movement that is passively guided (Adamovich et al. 1998; Bhanpuri et al. 2013; Fuentes and Bastian 2010; Gritsenko et al. 2007; Laufer et al. 2001; Monaco et al. 2010). There is a case, however, of self-generated movement that is not directly driven by active muscle contraction. In multijoint systems like the upper limb, motion of one limb segment about a joint can be driven passively by rotational forces that arise due to rotation of an adjacent limb segment about another joint (Gribble and Ostry 1999; Hollerbach and Flash 1982). We exploited differences in interaction torque profiles between different types of upper limb motion (*‘whipping’* or *‘reaching’*) to address the question of whether limb position sense in humans is influenced by intersegmental dynamics. Specifically, we investigated whether limb position sense during rotation about a joint differed depending on whether motion about that joint was driven primarily by active muscle torque or passive interaction torque.

4.1 Higher Proprioceptive Acuity for ‘Reaching’ Movements

We found that uncertainty ranges (URs), which are inversely related to proprioceptive acuity, were significantly lower in the ‘*reaching*’ condition than the ‘*whipping*’ condition. Participants’ perceived sense of limb position during elbow-joint perturbations was therefore more sensitive to actual limb position when elbow motion was primarily driven by interaction torque than when it was primarily driven by active muscle torque. This finding is at odds with our original prediction that proprioceptive acuity would be higher during muscle torque-driven ‘*whipping*’ movements than during interaction torque-driven ‘*reaching*’ movements. In previous research concerning proprioceptive acuity during self-generated or passively-guided movements, the presence of alpha-gamma coactivation is commonly cited as a potential explanation for why proprioceptive acuity has been found to be higher when motion is driven by voluntary muscle contraction. Since alpha-gamma coactivation maintains spindle sensitivity during self-generated muscle contraction, but not during passively/externally guided movement, we expected that elbow muscle spindles might have greater discharge and thus higher sensitivity to changes in limb position during the ‘*whipping*’ movement. This expected result would have been consistent with the findings of most studies of active versus passive proprioception; however, we found the opposite of what we expected. Our findings suggest that, at the level of an individual joint, proprioceptive acuity was better during passive interaction torque-driven motion than during motion driven by active muscle torque.

It is important to note that the *‘reaching’* movement used in our study did not involve entirely passive elbow rotation. Some muscle torque was still produced at the elbow, but in significantly lower amounts than for the *‘whipping’* movement (Figure 2C). While it is perhaps possible that the presence of any muscle torque at the elbow was sufficient to preserve proprioceptive acuity in the *‘reaching’* condition by alpha-gamma coactivation, this would not account for the superior acuity we observed during *‘reaching’* movements (Figure 6).

Another important distinction between the *‘reaching’* movement used to test ‘passive’ proprioception in this study and the passive movements typically used in previous studies is that our *‘reaching’* movement was self-generated, whereas the passive movements in the literature have been passively-guided/externally-generated. To explain why proprioceptive acuity might be higher for self-generated than passively-guided movements, authors of previous work have also proposed that during self-generated movements, an efference copy of the descending motor command is used to generate central estimates of limb position which, when used in combination with sensory feedback, improve proprioceptive acuity relative to when sensory feedback alone is used (e.g., see Paillard and Brouchon 1968). According to this explanation, then because our ‘passive’ movement was self-generated, the potential use of a forward model by the central nervous system to generate estimates of arm position might have contributed to preserving acuity at the elbow joint.

A third potential consideration in light of our findings is the possibility that the central nervous system might differentially modulate afferent pathways during self-generated motion based on anticipated interaction torque profiles. It is known that the motor system uses anticipatory mechanisms, based on learned representations of musculoskeletal and task-specific dynamics, to compensate for interaction torques in a predictive manner (Gribble and Ostry 1999; Sainburg et al. 1999)—that is, the central nervous system anticipates interaction torques and predictively adjusts neural control signals to muscles to compensate for them. It is therefore known that the brain accurately predicts when motion about a joint will occur as a consequence of interaction torque. It has also been shown that primary Ia muscle spindle receptors are modulated in a goal-dependent manner during movement preparation (Papaioannou and Dimitriou 2021). The authors found that this modulation occurred in the absence of any changes to muscle kinematics or electromyographic signals, and proposed that this effect was mediated by independent fusimotor control of the muscle spindle afferents. Given the critical role that proprioception plays in the control of intersegmental dynamics (Ghez and Sainburg 1995; Sainburg et al. 1993, 1995, 1999), perhaps the motor system predictively modulates spindle sensitivity (e.g., via fusimotor control) when preparing for movements that involve high interaction torques. In theory, this might preserve or enhance proprioceptive sense during motion that is not primarily driven by muscle contraction. Alternatively—or perhaps, additionally—the improvement in proprioceptive acuity that we observed for *‘reaching’* movements relative to *‘whipping’* movements could also be mediated through differences in cortical processing.

4.2 Limitations

4.2.1 Servo Controller

The controller we used to produce servo-controlled position perturbations often made poor predictions of unperturbed elbow angle, which sometimes resulted in the generation of inappropriate perturbations that needed to be excluded from analyses (see section 2.4.3). Although the consistency of the perturbations was improved by increasing the number of velocity profiles that were stored for matching purposes (see section 2.3.3.4), several trials still needed to be excluded for each participant (*M* = 25.93 of 128 non-sham perturbations across *‘whipping’* and *‘reaching’* conditions, *SD* = 6.19). We accounted for this by including an excess number of perturbation trials (64 non-sham perturbations per experimental block) in the task design; however, to balance the need for more perturbation trials with the risk of influencing behaviour, we also included several non-perturbation trials, such that participants were perturbed only 20% of the time (consistent with other studies such as Darainy et al. 2004, 2006, 2007; Lametti et al. 2007; Wong et al. 2009). As a result, participants performed over 1000 reaches (including training) in a single session lasting up to two hours. The use of a servo controller that generates more accurate predictions about the unperturbed elbow trajectory—and therefore more consistently produces appropriately shaped and sized perturbations—would be of benefit for improving the viability of single trials and reducing the overall length of the testing session.

4.2.2 Amplitude and Velocity of Elbow Rotation

This work is limited by significant differences in the amplitude and velocity of rotation about the elbow between ‘*reaching*’ and ‘*whipping*’ movements. As described in section 1.3, the ‘*reaching*’ and ‘*whipping*’ movements were designed to be identical in terms of the direction of elbow rotation, total distance reached, and reach duration; however, a consequence of this design was that the total amplitude of rotation about the elbow during the ‘*reaching*’ movement was greater than that during the ‘*whipping*’ movement. Given that the reach time constraints for both movements were the same, unequal amounts of elbow rotation produced differences in elbow velocity, and elbow velocity was consequently higher for the *‘reaching’* movement than the *‘whipping’* (see section 2.3.2). Given that muscle spindle afferents signal both the amount and velocity of muscle stretch, perhaps it is possible that differences in the speed of joint rotation (and therefore velocity of muscle stretch) prior to receiving a position perturbation at that joint might influence position sense. Although we found no evidence of a relationship between the speed of rotation about the elbow joint and proprioceptive acuity in this task (see section 3.2), it should be noted that we did not experimentally manipulate the speed of elbow rotation, and that the present study involved only a small sample of participants whose angular elbow speeds spanned a limited range that was constrained by the nature of the task. Future studies may wish to investigate in a controlled manner the potential influence of the speed of joint rotation on position sense at that joint.

4.3 Future Directions

Our findings raise interesting questions about the influence of intersegmental dynamics on limb position sense. First, it is important to reproduce the findings of this study with *‘reaching’* and *‘whipping’* movements that are matched with respect to amplitude and velocity of rotation about the elbow joint. This will address the question of whether the difference in proprioceptive acuity that we observed was a consequence of increased elbow velocity during the *‘reaching’* movement. It should be noted, however, that because interaction torques increase with reach velocity (Hollerbach and Flash 1982), if proprioceptive processing is modulated according to anticipated interaction torque profiles (see section 4.1), an increase in velocity might influence proprioceptive acuity through its influence on intersegmental dynamics. For example, it is possible that at low velocities proprioceptive acuity is better for muscle torque-driven movements than interaction torque-driven movements, yet at high velocities the opposite could be true. Future studies should therefore explore the relationship between elbow velocity, interaction torques, and proprioceptive acuity.

Another interesting avenue for future research is to investigate the extent to which afferent input from the shoulder might be used for sensing elbow position during movements where elbow motion is driven primarily by interaction torque arising from active shoulder motion. Just as motion about the shoulder joint can produce interaction torque at the elbow, motion at the elbow can also produce interaction torque at the shoulder. Future work might investigate the possibility that interaction torque generated at the shoulder by the application of a single-joint perturbation to the elbow contributes to our perception of limb position at the elbow.

Lastly, if the motor system does in fact predictively modulate pathways for proprioceptive processing in anticipation of interaction torques, future studies may seek to investigate on what level this modulation occurs. In section 4.1 we have outlined a potential mechanism whereby spindle sensitivity may be modulated by fusimotor control; however, it is also possible that intersegmental dynamics-related differences in proprioceptive acuity are mediated by differences in cortical processing of afferent input. For example, perhaps inputs from spindles across different muscles, inputs from other (non-spindle) types of proprioceptors, and central estimates of limb position based on corollary discharge, are differentially weighted in computations of limb position during movements involving high or low interaction torques. This may occur by a predictive mechanism in which different sources of sensory input are reweighted in an anticipatory manner, following the instantiation of existing neural representations of movement dynamics (e.g., when performing a movement that involves high interaction torques). Such a hypothesis could perhaps be tested by evaluating proprioceptive acuity in a task in which some types of afferents are anesthetized, or in which there is a discrepancy between the information provided by one proprioceptor and another (e.g., an illusory manipulation such as tendon vibration could help isolate the contribution of one muscle to limb position sense). Since the magnitude of interaction torques during reaching correlates highly with movement direction, future research could also investigate whether there are direction-dependent changes in neural activation patterns in somatosensory regions during movement. Of primary interest is Brodmann Area 3A, which receives afferent input from peripheral proprioceptors and is thought to subserve proprioceptive sense.

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