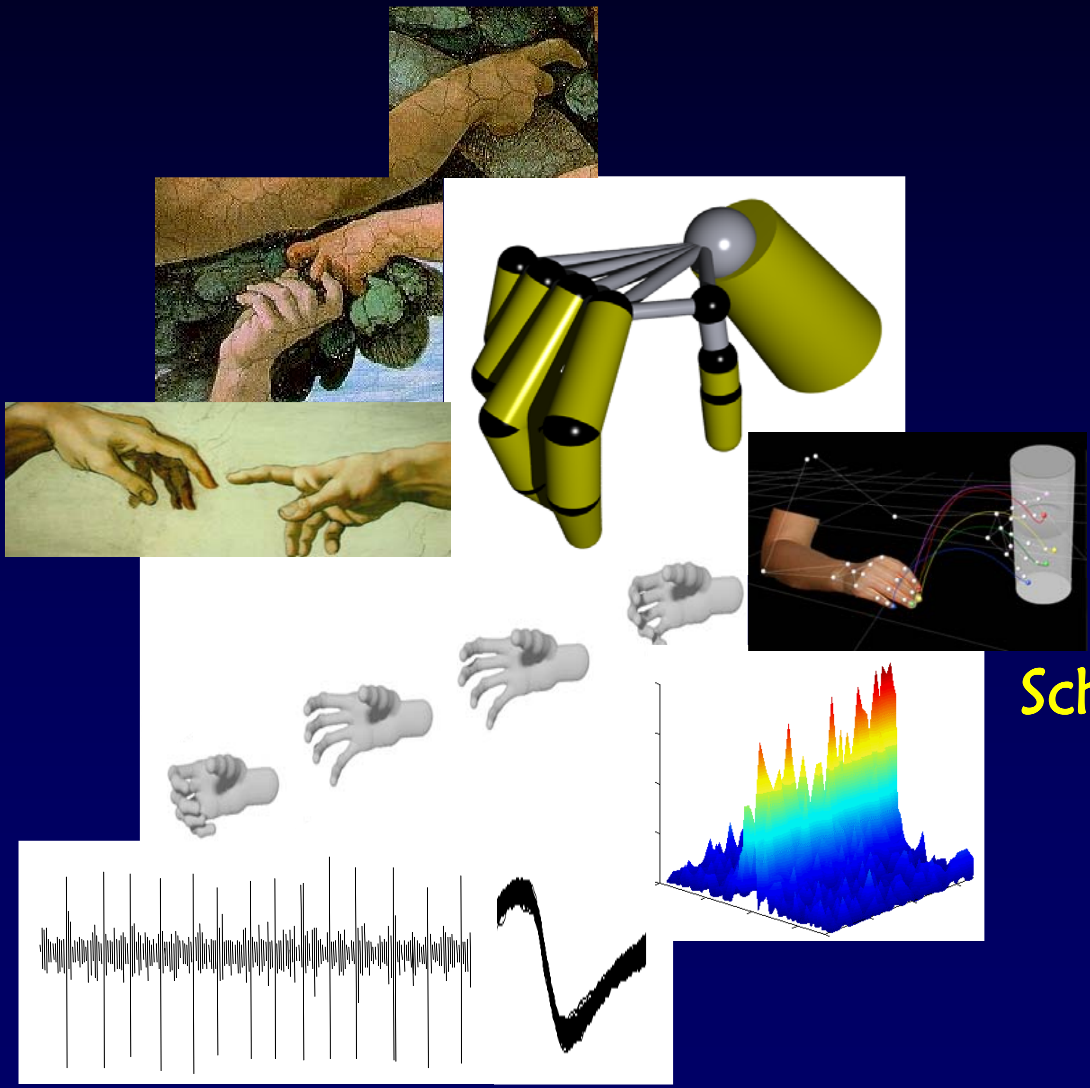
Neural Control of the Hand: Learning and Control



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Outline

Introduction

- The Human Hand
  - Biomechanics
  - Neural control

Neural control of hand muscles

- Common Neural Input
  - Motor unit synchrony
  - EMG-EMG coherence

Learning Object Grasping and Manipulation

- Anticipatory Grasp Control
  - Sensorimotor memories
  - Control of digit forces and positions

Open questions

Introduction

The Human Hand

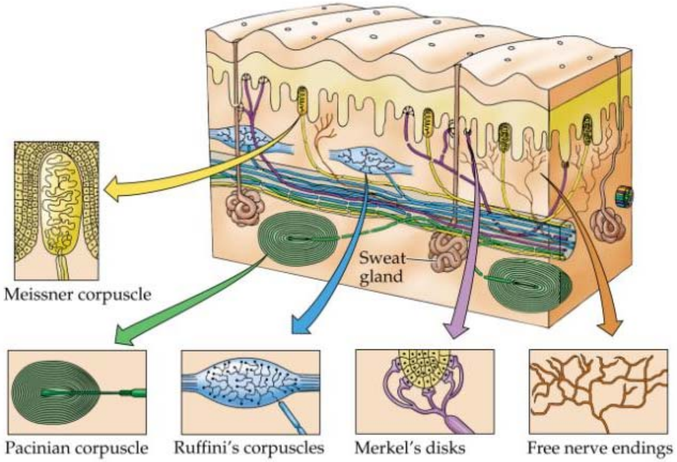
Biomechanics

Neural Control

The Human Hand

The hand is fundamental to sensorimotor development.

The **sensory** machinery of the hand allows to extract detailed knowledge about the environment we interact with.



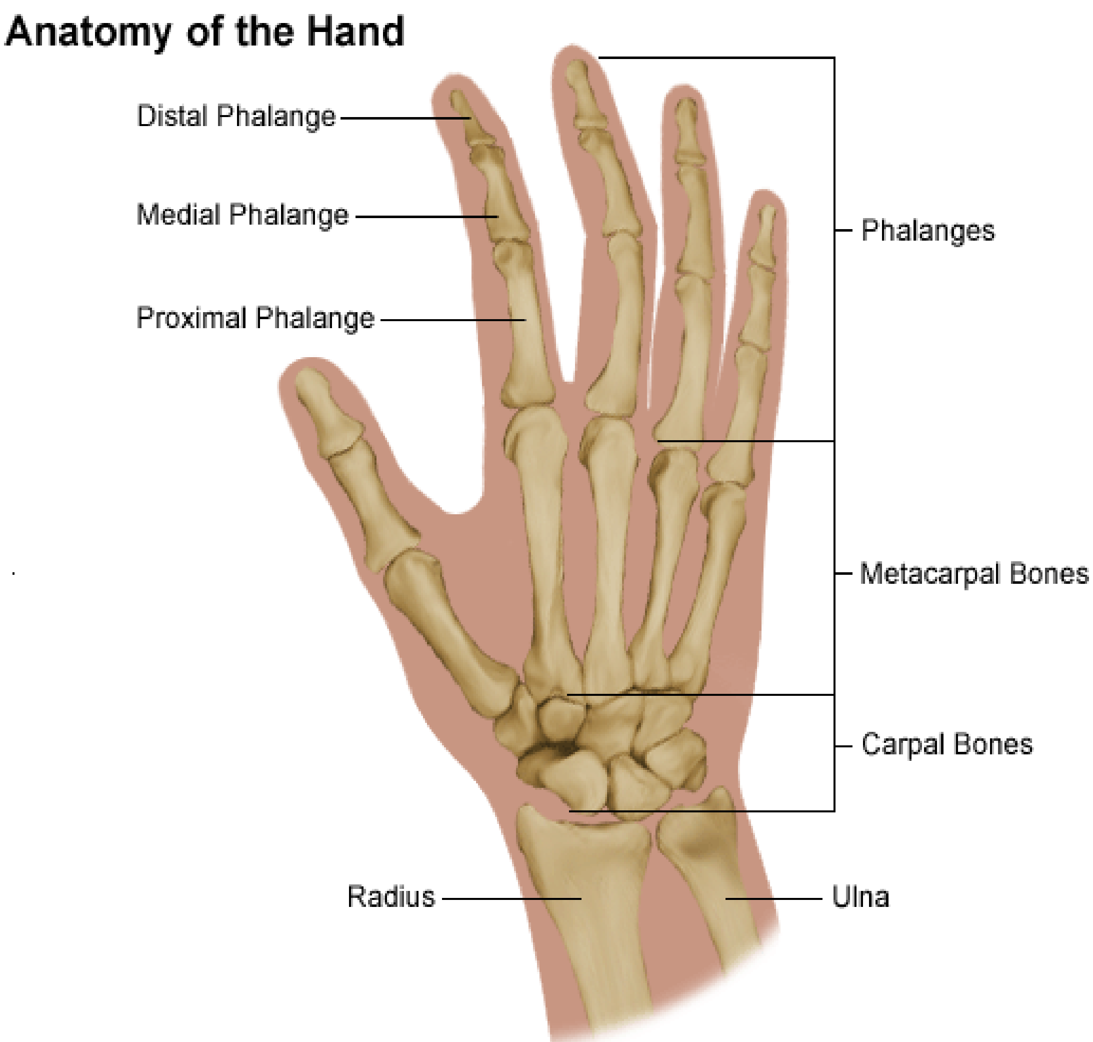
The unique versatility of the hand **motor** system enables highly dexterous control of a large repertoire of movements.

Why study the hand?

The complex neural and biomechanical architecture of the hand makes it an ideal model to study fundamental issues in neuroscience, such as:

- *sensorimotor transformations*
- *learning and control of complex movements*
- *neuroplasticity*
- *neuroprosthetics, robotics*

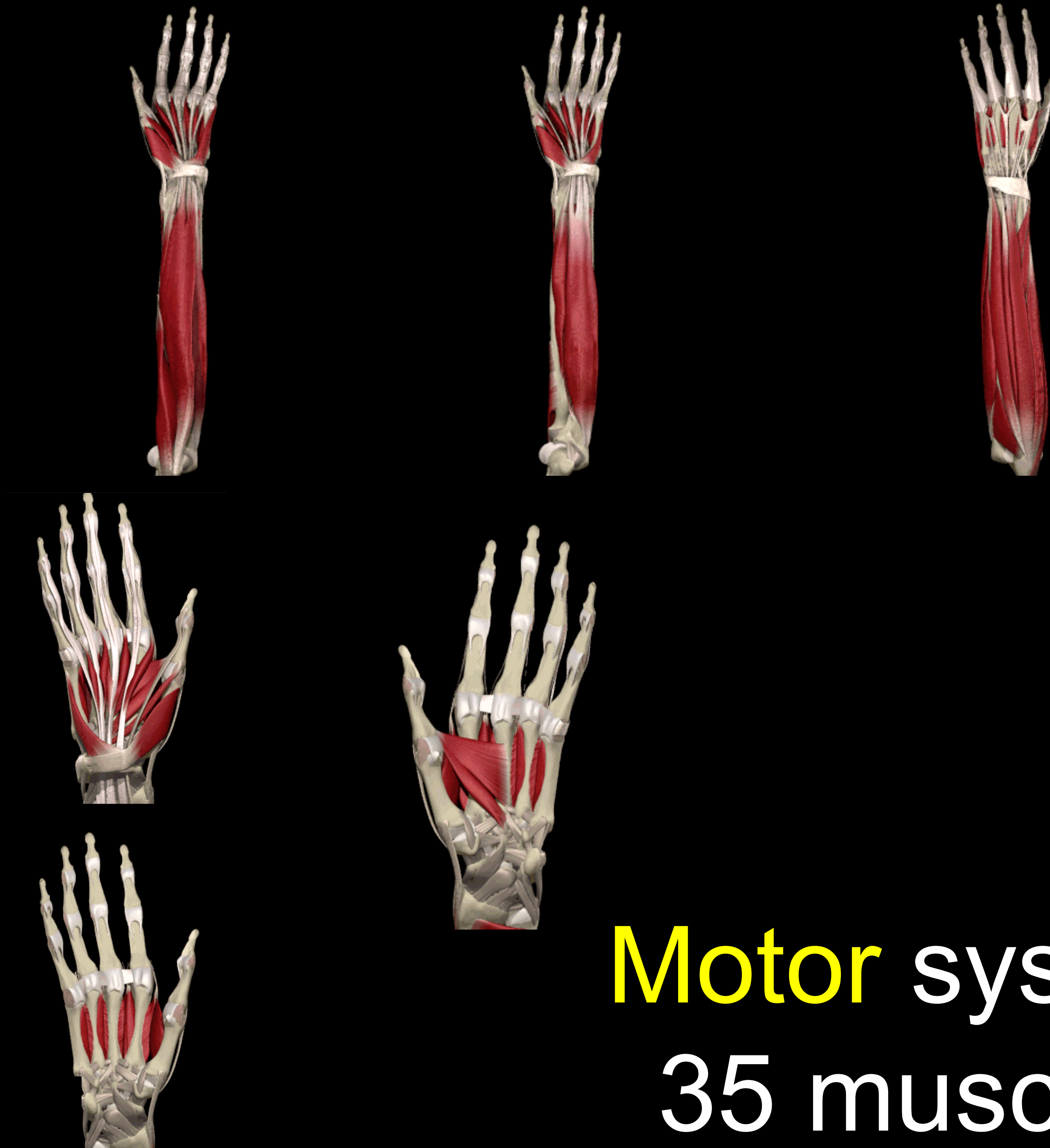
The Human Hand: Biomechanics



27 bones

extrinsic

intrinsic

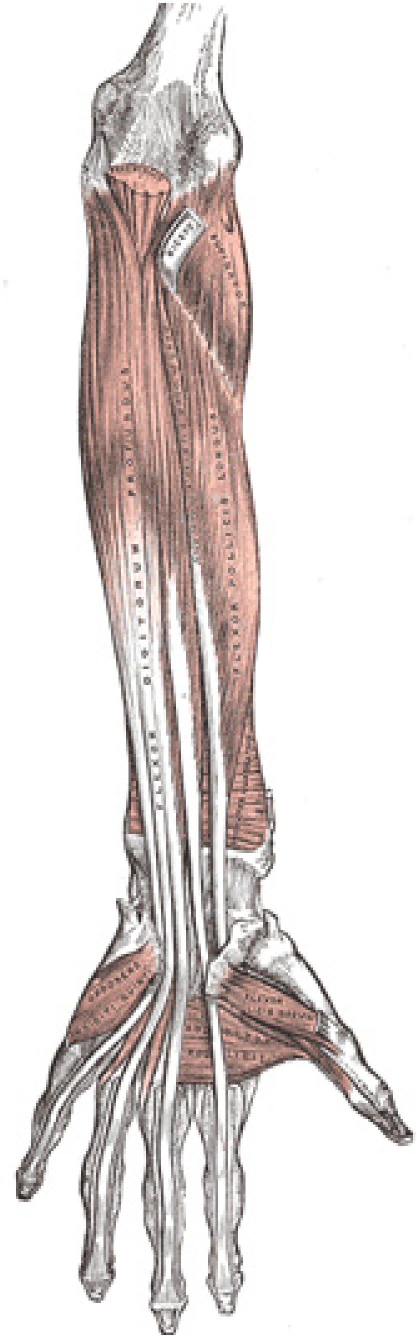


Motor system
35 muscles

- **Large number of joints and muscles, some of which cross more than one joint**

Implications for control:

- Large number of control variables = large ‘computational load’ on the CNS
- Activation of a given muscle will generate motion at more than one joint

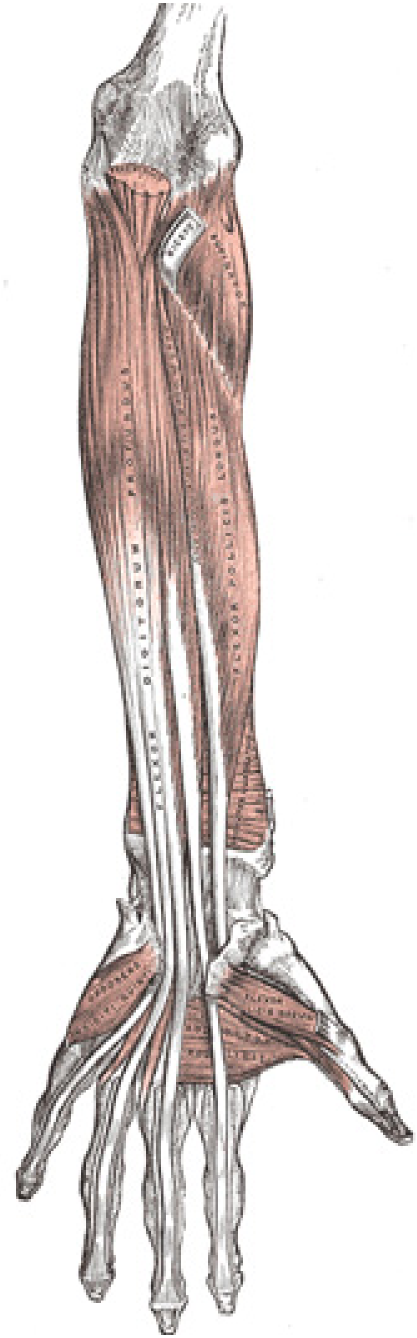


- **Connections among tendons of finger flexor and extensors**

Implications for control:

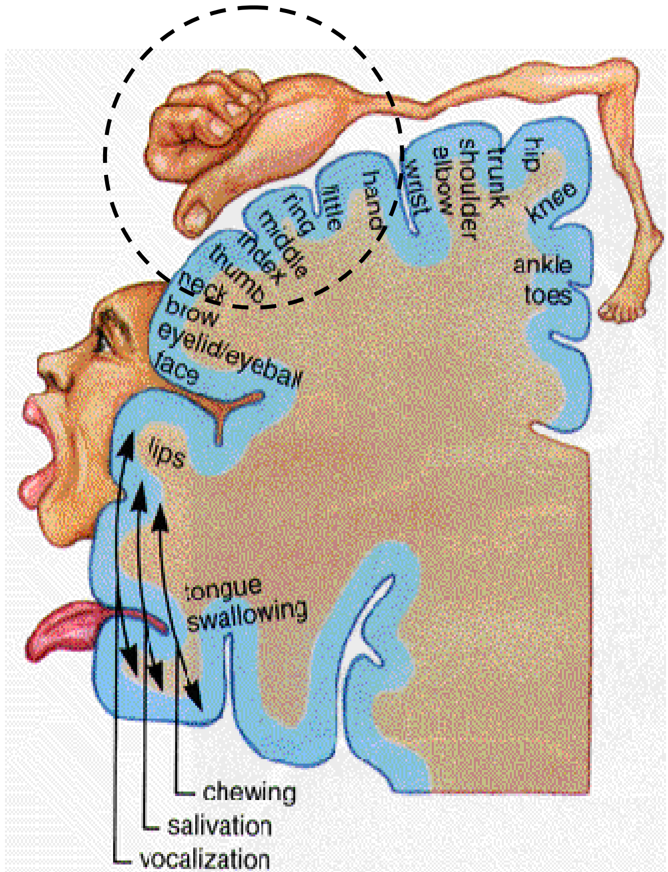
- Tension generated by the activation of a muscle inserting into one digit will be passively trans-mitted to the tendons inserting into adjacent digits

- Producing independent finger movement or force requires the ability to limit such ‘spill-over’ of tension to non-instructed digits

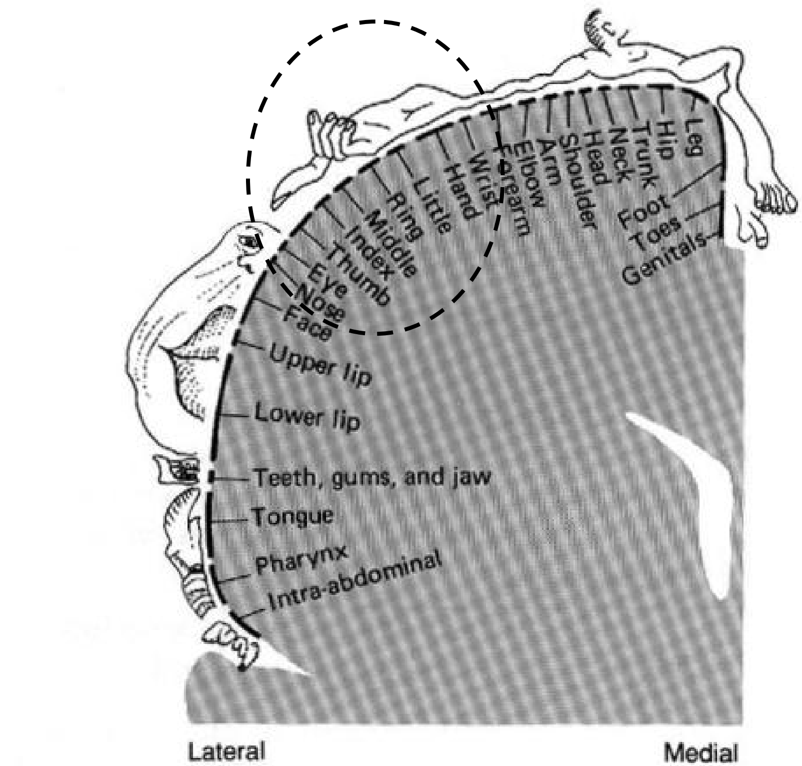


The Human Hand: Neural Control

Motor Area



A Sensory homunculus



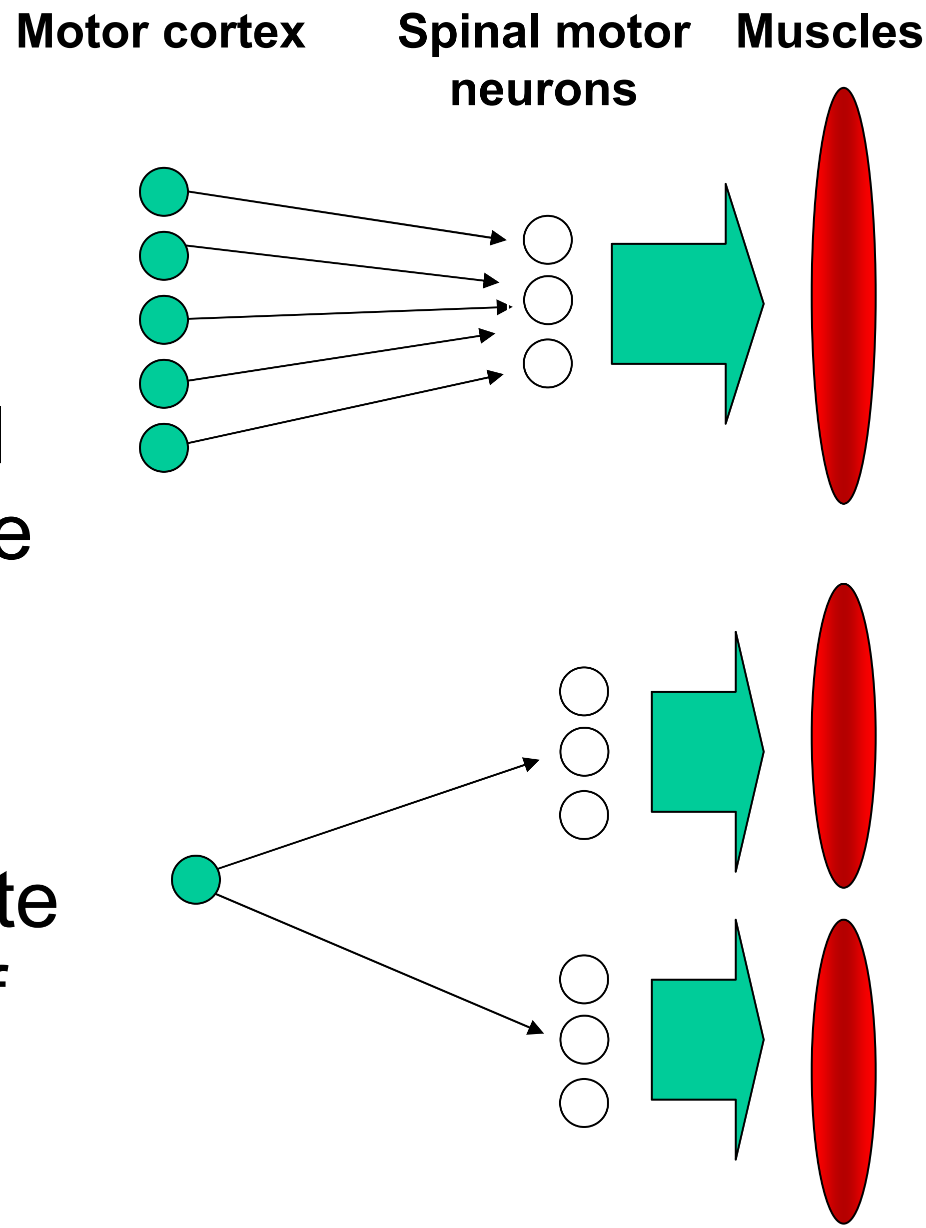
Somatotopical organization of motor and sensory cortex

However, anatomical and physiological evidence indicate that the cortical representation of hand muscles in M1 is ***not*** somatotopically organized.

Cortical territories in M1 occupied by cortico-motoneuronal cells for different thumb and finger muscles overlap extensively (e.g., Schieber and Hibbard 1993; Rathelot and Strick 2006).

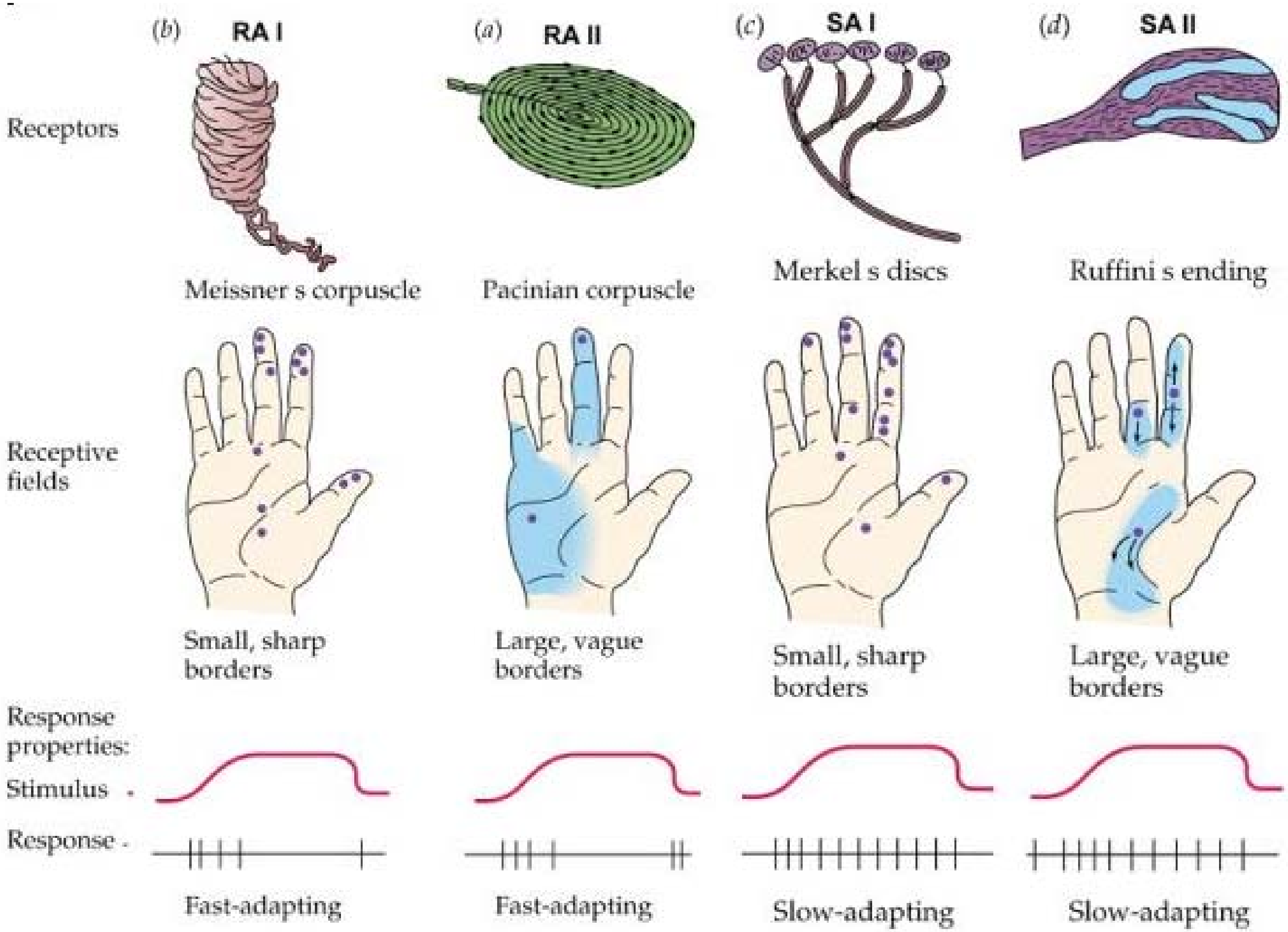
- Outputs of large territories of the motor cortex **converge** on the spinal motor neuron pool of any given hand muscle

- Output projections of single cortical neurons often **diverge** to innervate the motor neuron pool of more than one muscle.



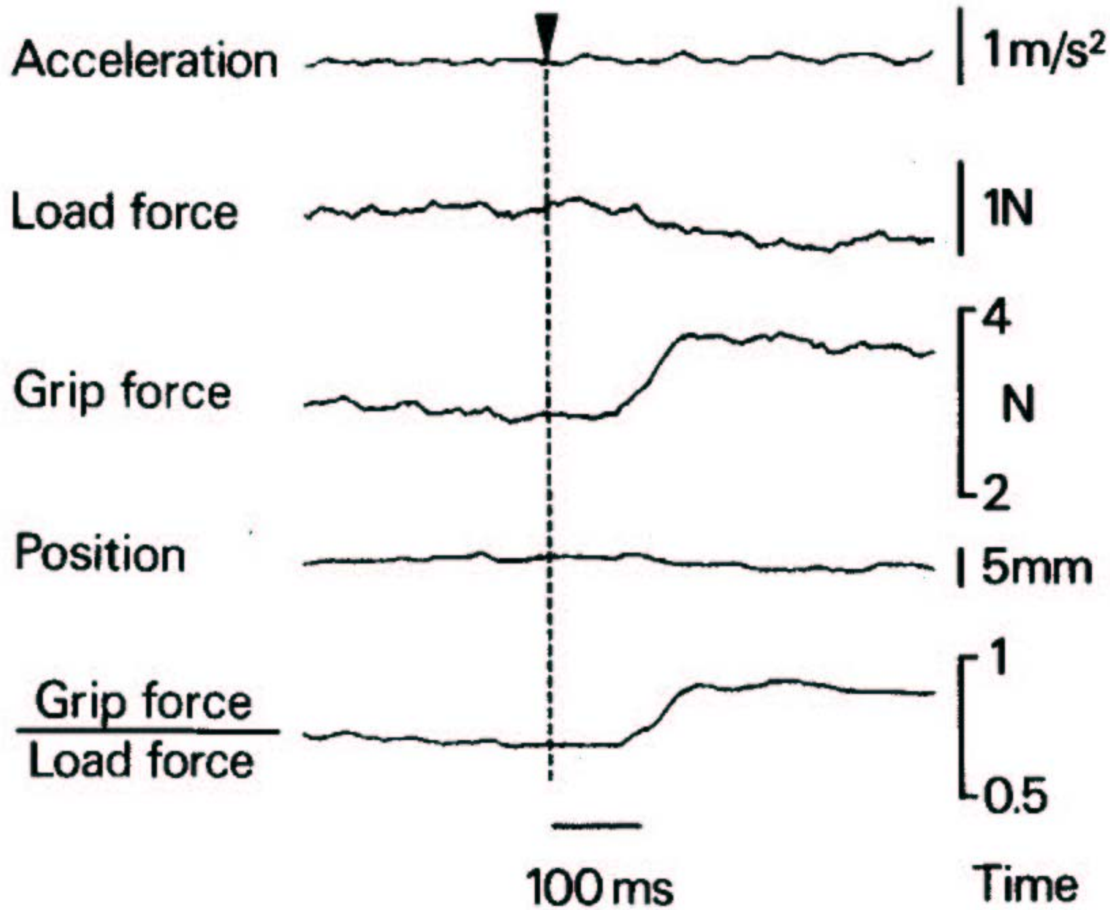
Sensory system

Mechanical stimuli are encoded by tactile afferents that differ in their sensitivity to specific aspects of the stimuli.

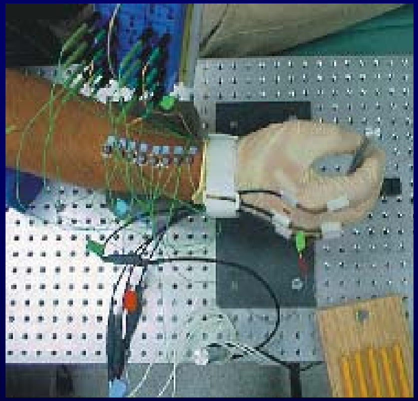
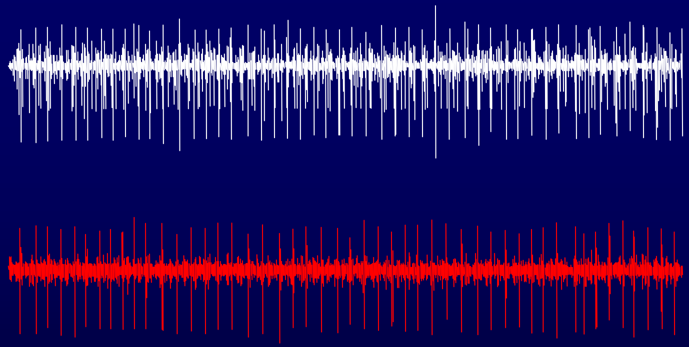


Tactile input about micro-slips trigger very fast upgrades in the ratio between grip and load forces.

Besides its ‘online correction’ functions, tactile input allows to build **‘sensorimotor memories’** for *anticipatory control* of grasping.



Johansson and Westling (1987)


Neural control of hand muscles

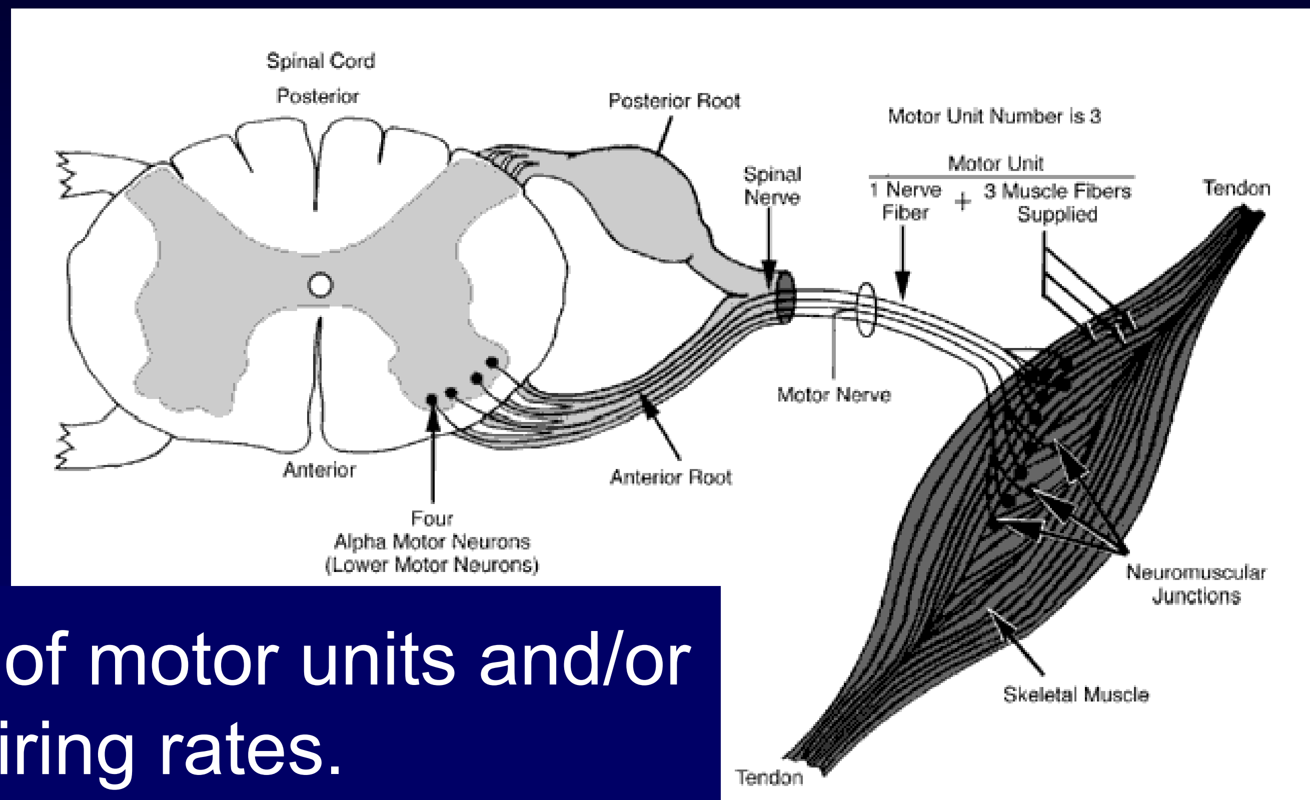
Common Neural Input

Motor unit synchrony

EMG-EMG coherence

Coordination of single motor unit activity during grasping

Motor units are the basic unit of force control. Force modulation can be attained by recruiting a variable number of motor units and/or increasing their firing rates.



One of the neural mechanisms that might contribute to the coordination of forces during grasping is **motor unit synchrony**.

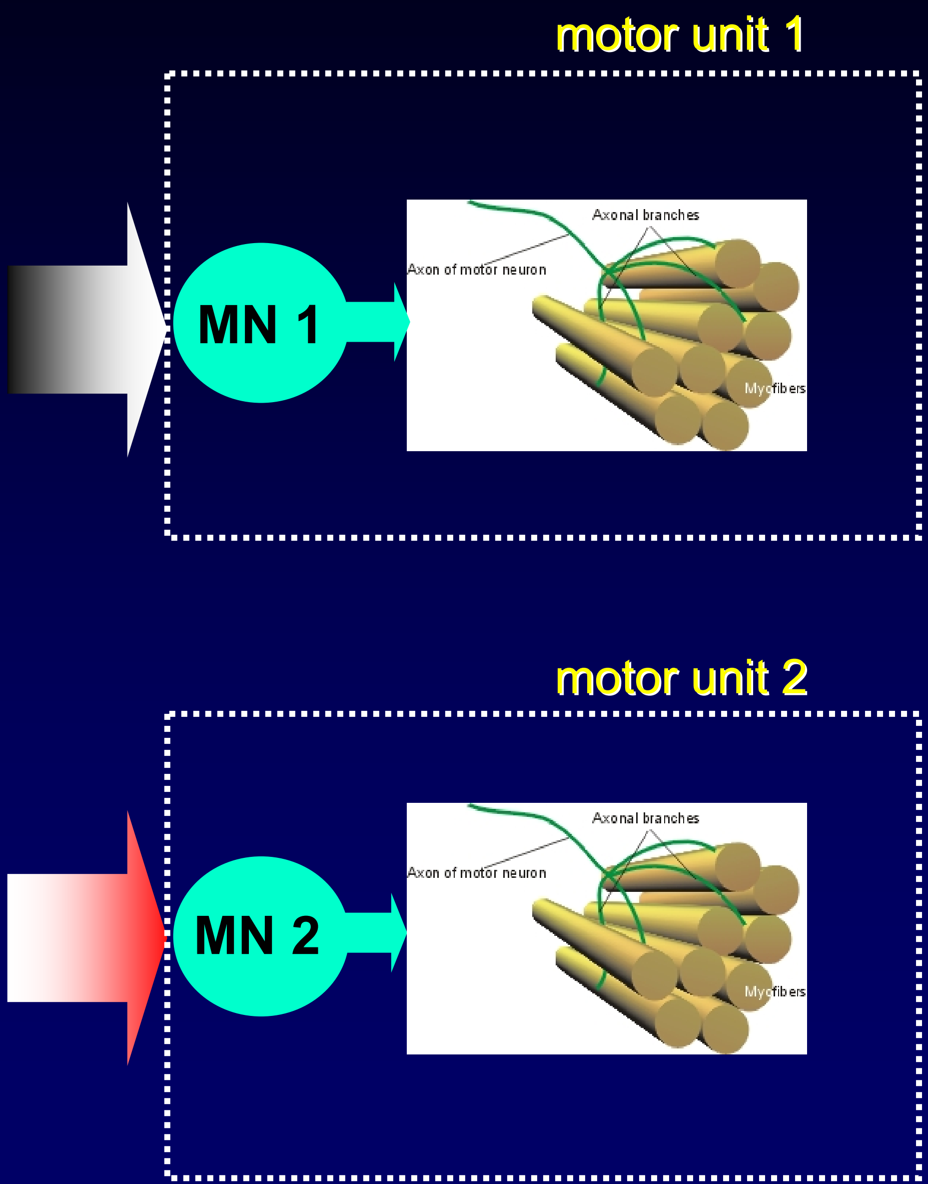
A generally accepted view is that short-term synchrony of active motor units is an indirect measure of common synaptic input across motoneurons.

Sears and Stagg, J. Physiol. (1976)
Kirkwood and Sears, J. Neurosci. Meth. (1978)
Nordstrom et al. J. Physiol. (1992)

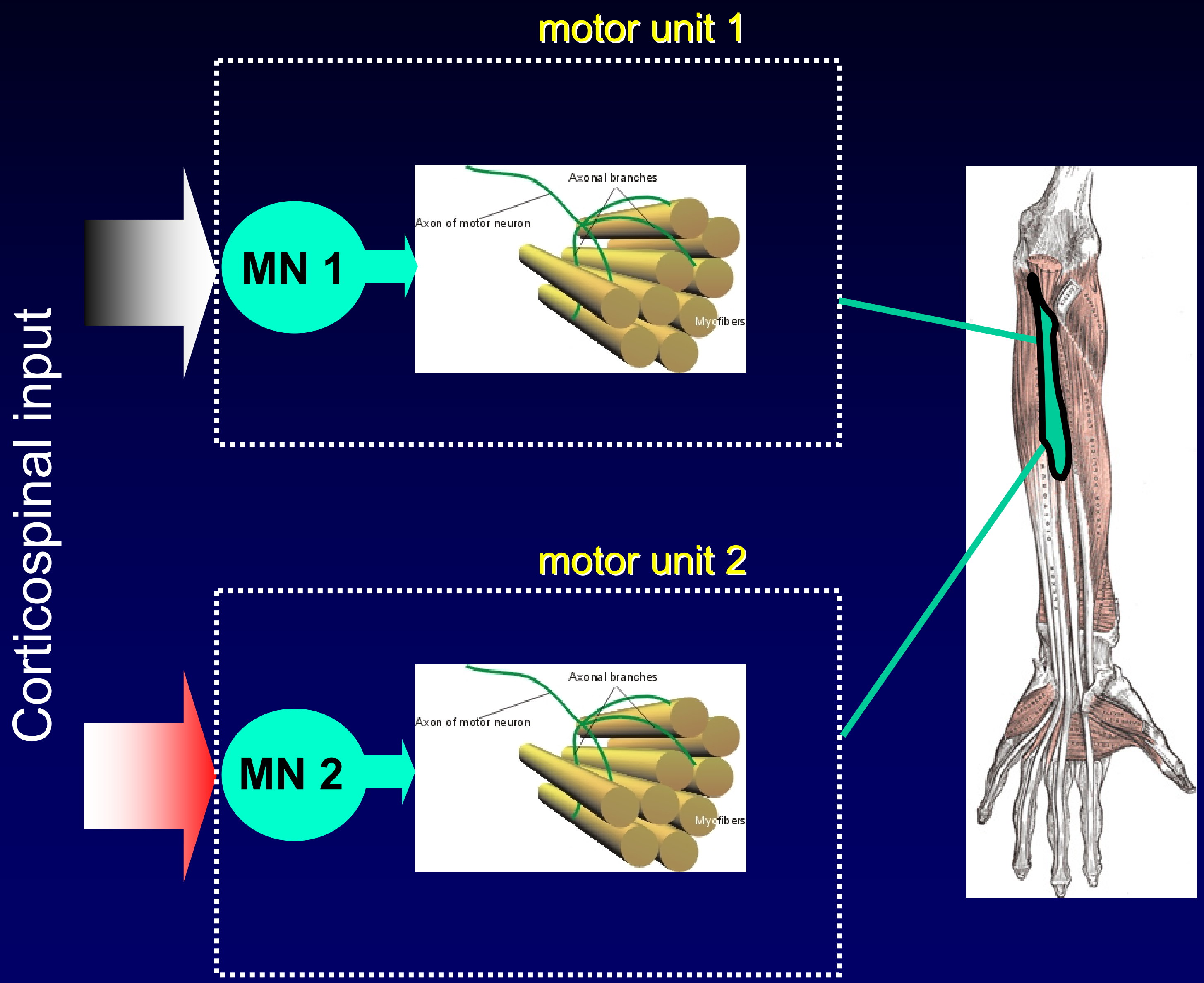
Neural input to motoneurons of hand muscles

Hand muscle motor units

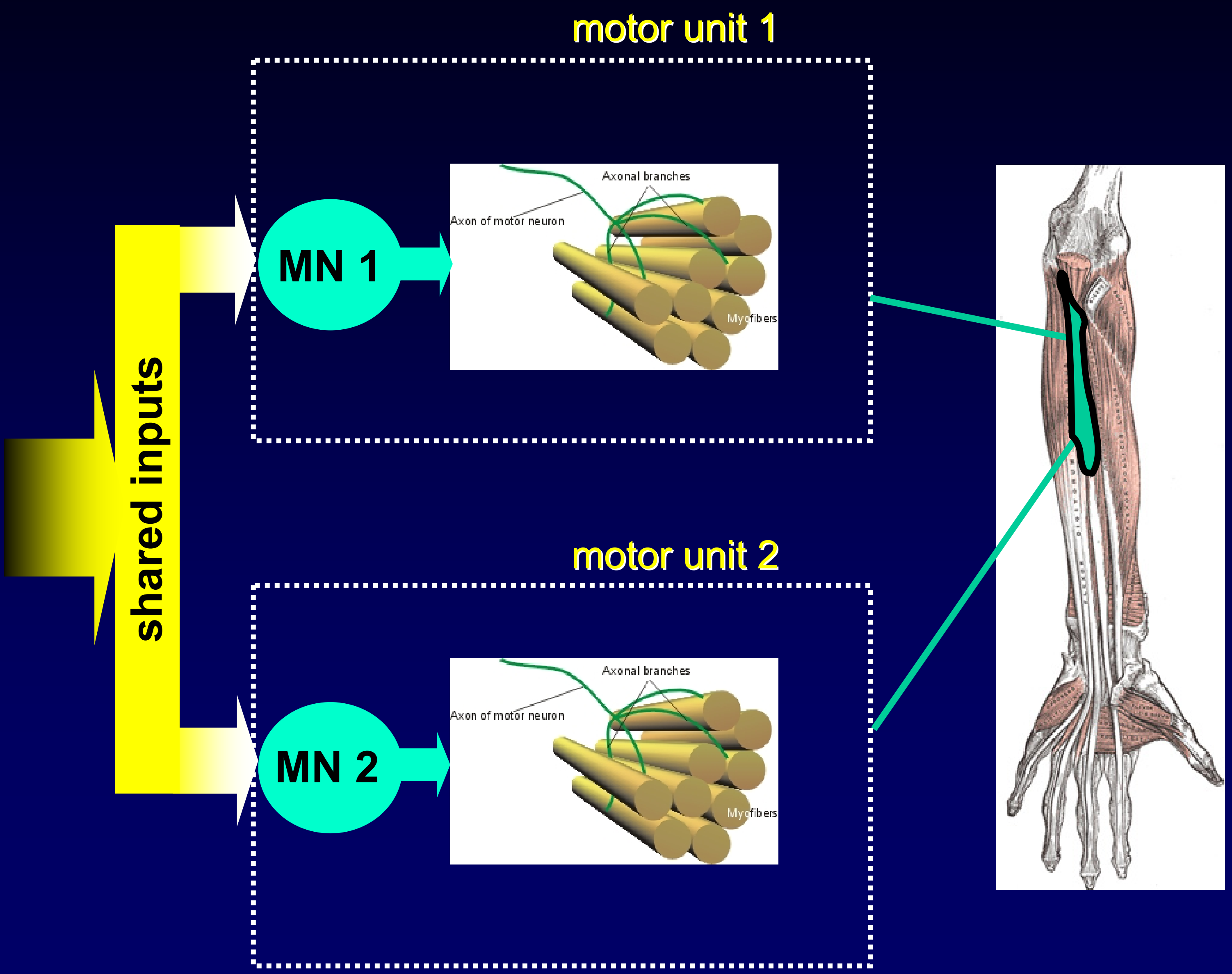
Corticospinal input



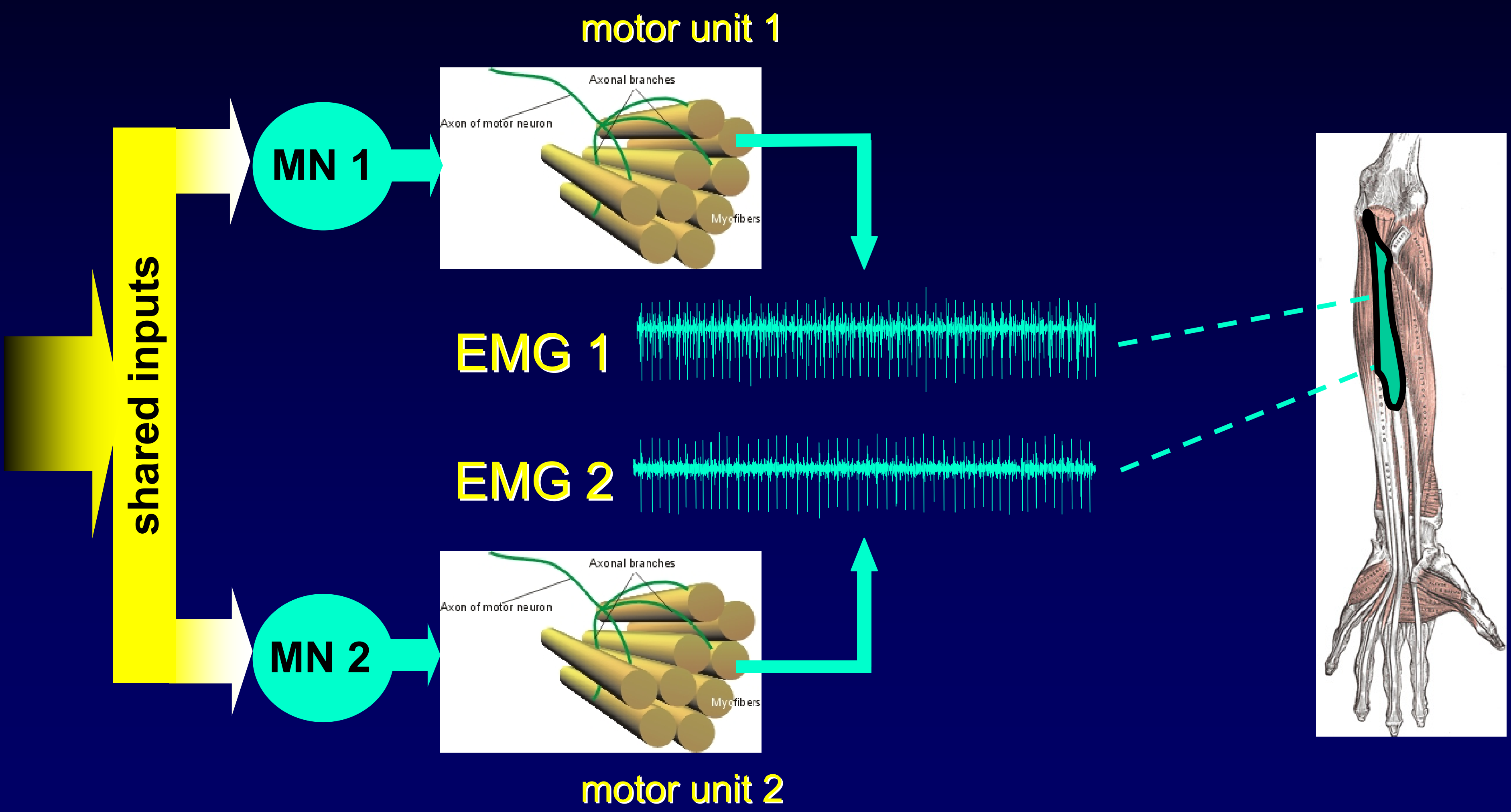
Motor units of the same muscle



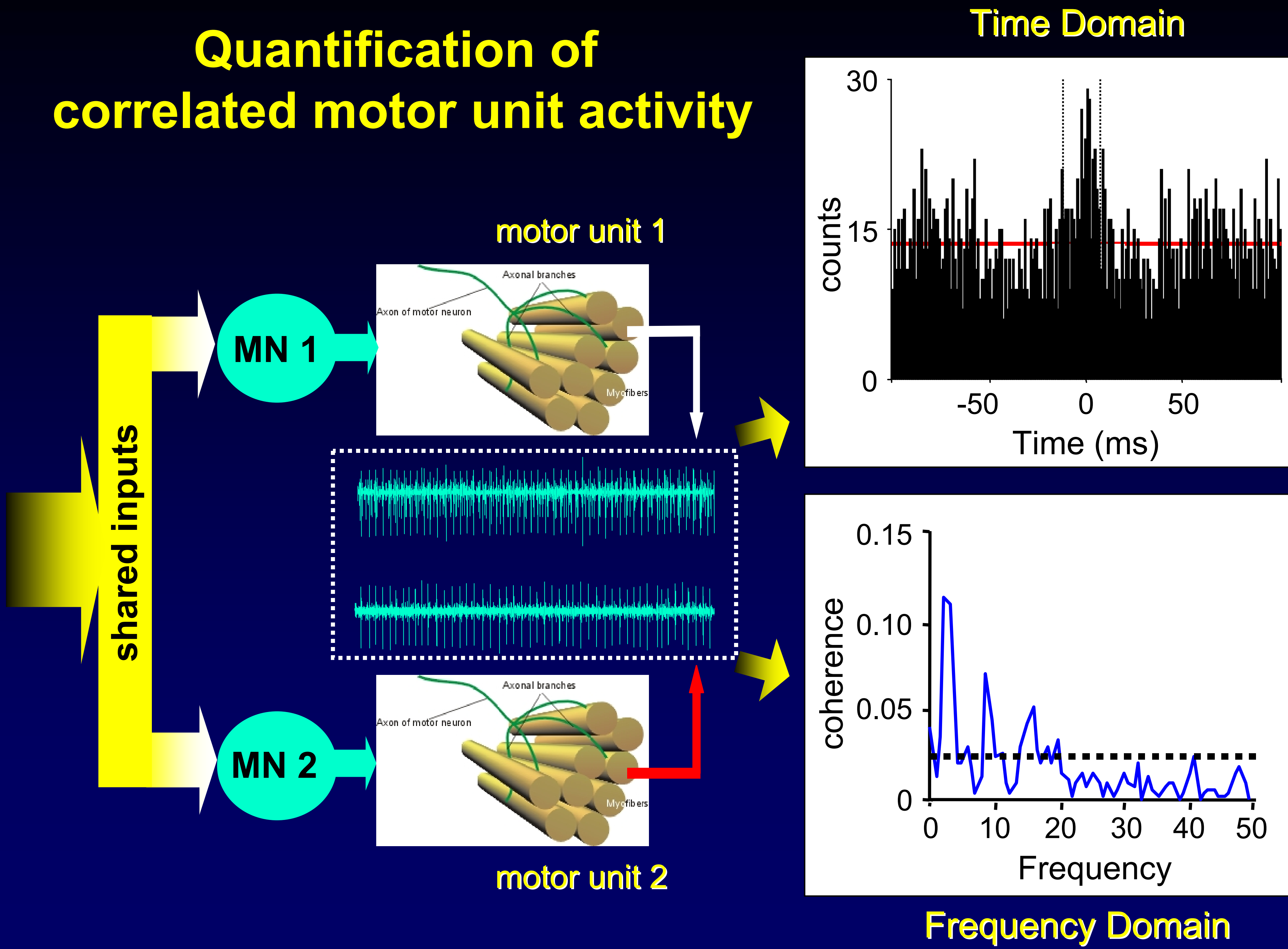
Common input to motor units of the same muscles (WITHIN-MUSCLE SYNCHRONY)



Single motor unit activity



Quantification of correlated motor unit activity



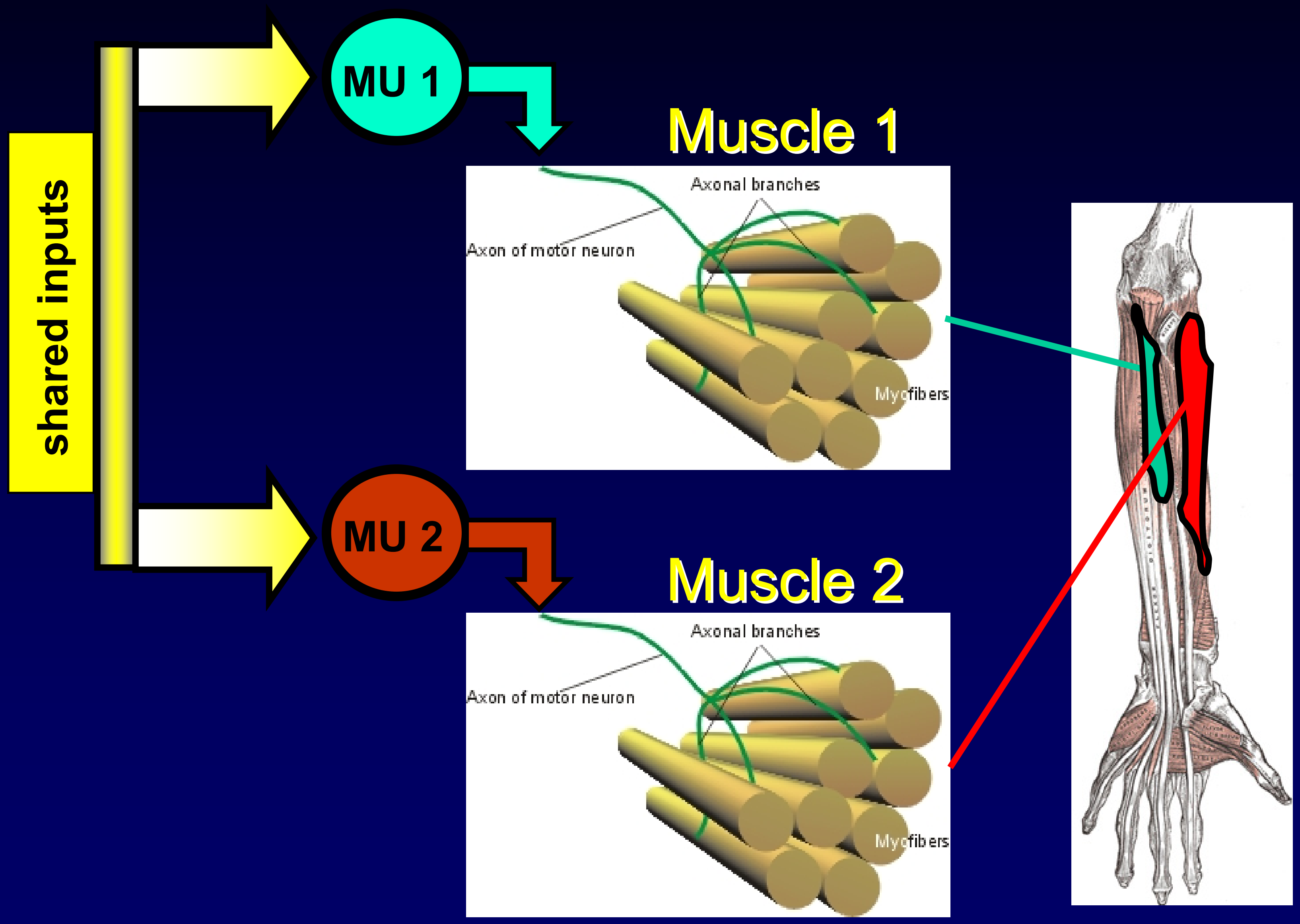
Correlated motor unit activity within the same muscle is a measure of how the activity of many motor units **of a given muscle** might be coordinated under certain conditions (e.g., isometric vs. eccentric contractions) or as a result of training (dexterity, strength, etc.).

e.g. Semmler et al., J. Neurophys. (2004)

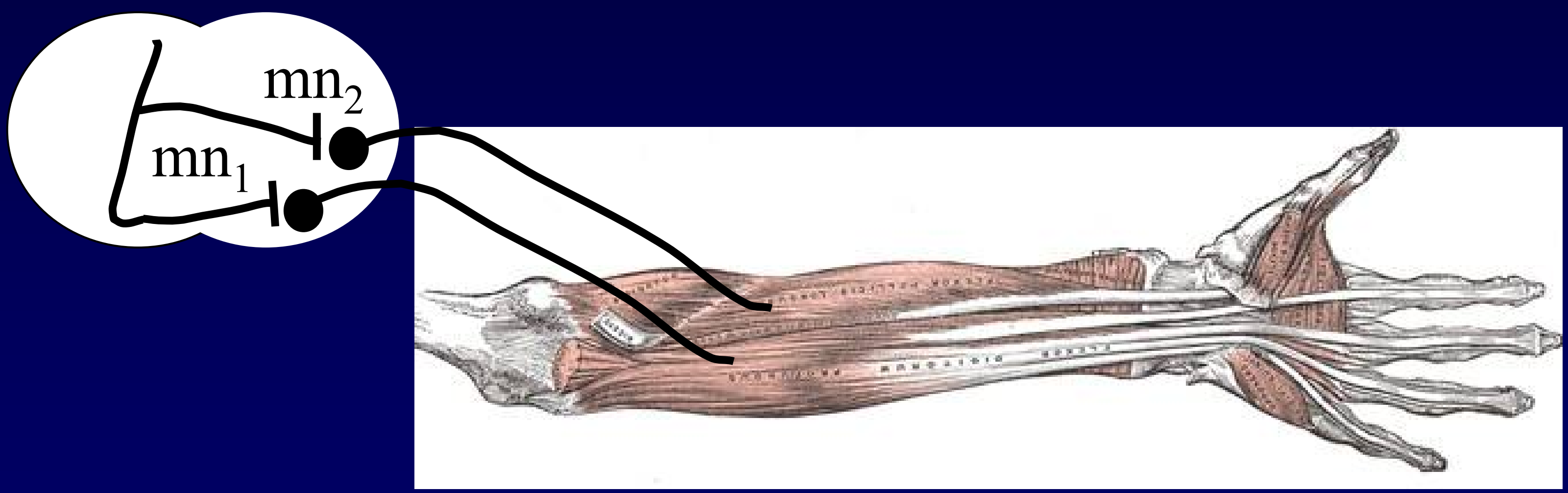
Synchronous activity can also occur across different muscles.

This type of synchrony (across-muscle) might play an important role for coordinating the activity of **different muscles**, e.g., flexor muscles of the the *thumb* and *index finger*.

ACROSS-MUSCLE motor unit synchrony



- Synchronous or near-synchronous discharges of motor units innervating different hand muscles/muscle compartments contributes to 'spill-over' of tension during individuated finger movements[1].

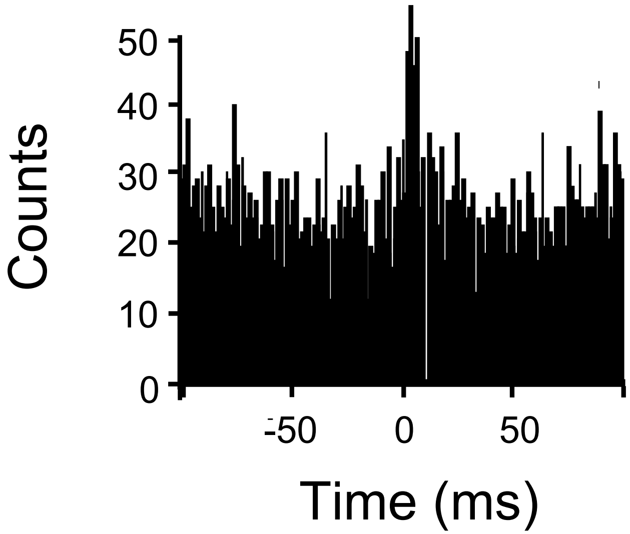


Keen and Fuglevand (2004); Reilly et al. (2004)

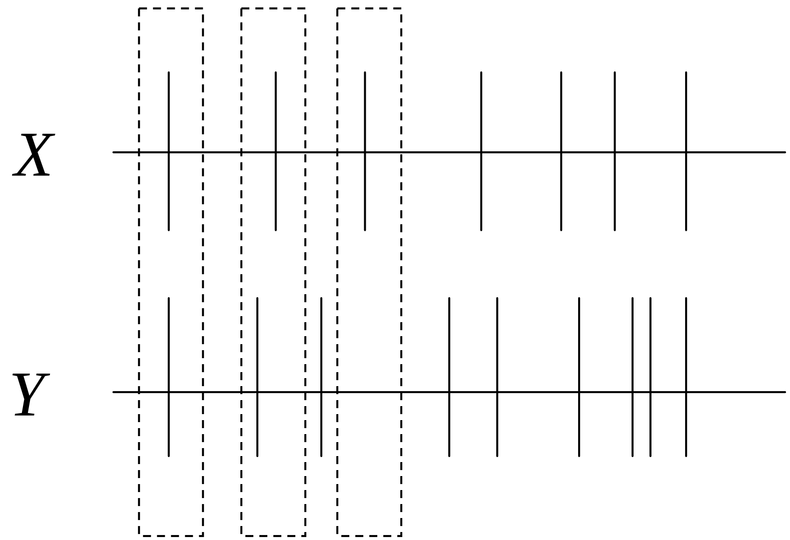
Correlations of neural activity

Correlation analysis of motor neuron activity has been used to determine the organization and connections of neurons that are otherwise inaccessible or difficult to record (Perkel et al. 1967).

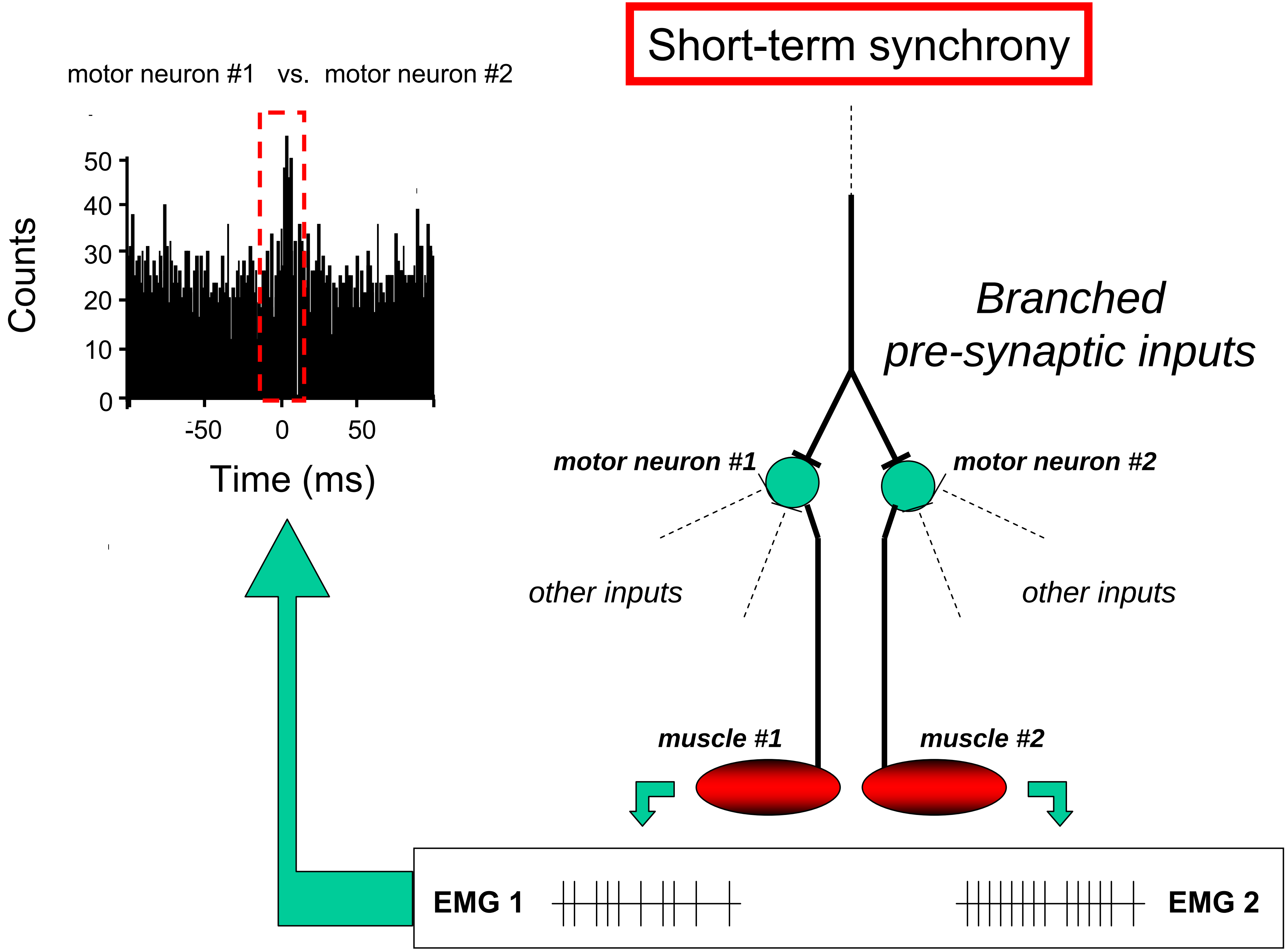
Correlation Analysis in the time domain



$$R_{YX}(\tau) = (1/T)\int y(t)x(t - \tau)dt$$

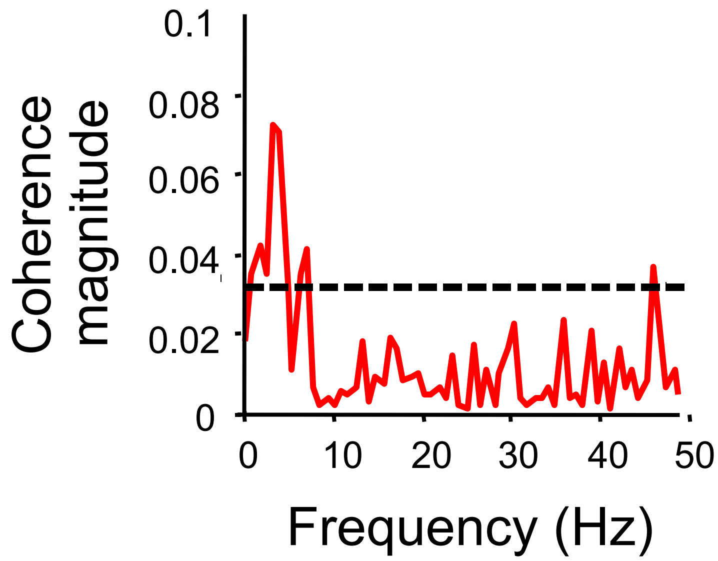


Correlation functions describe the dependence between two signals, *x* and *y*. By representing spike trains by values of **1** at times of spike occurrence and **0** at other times, $R_{YX}(\tau)$ is non-zero when spikes occur in both trains at an interval of τ. The cross-correlation histogram results from summations of the number of spikes in the two trains within a given time interval.



Short-term synchrony
motor neuron #1 vs. motor neuron #2
Counts
50
40
30
20
10
0
-50
0
50
Time (ms)
Branched
pre-synaptic inputs
motor neuron #1
motor neuron #2
other inputs
other inputs
muscle #1
muscle #2
EMG 1
EMG 2

Correlation analysis in the frequency domain



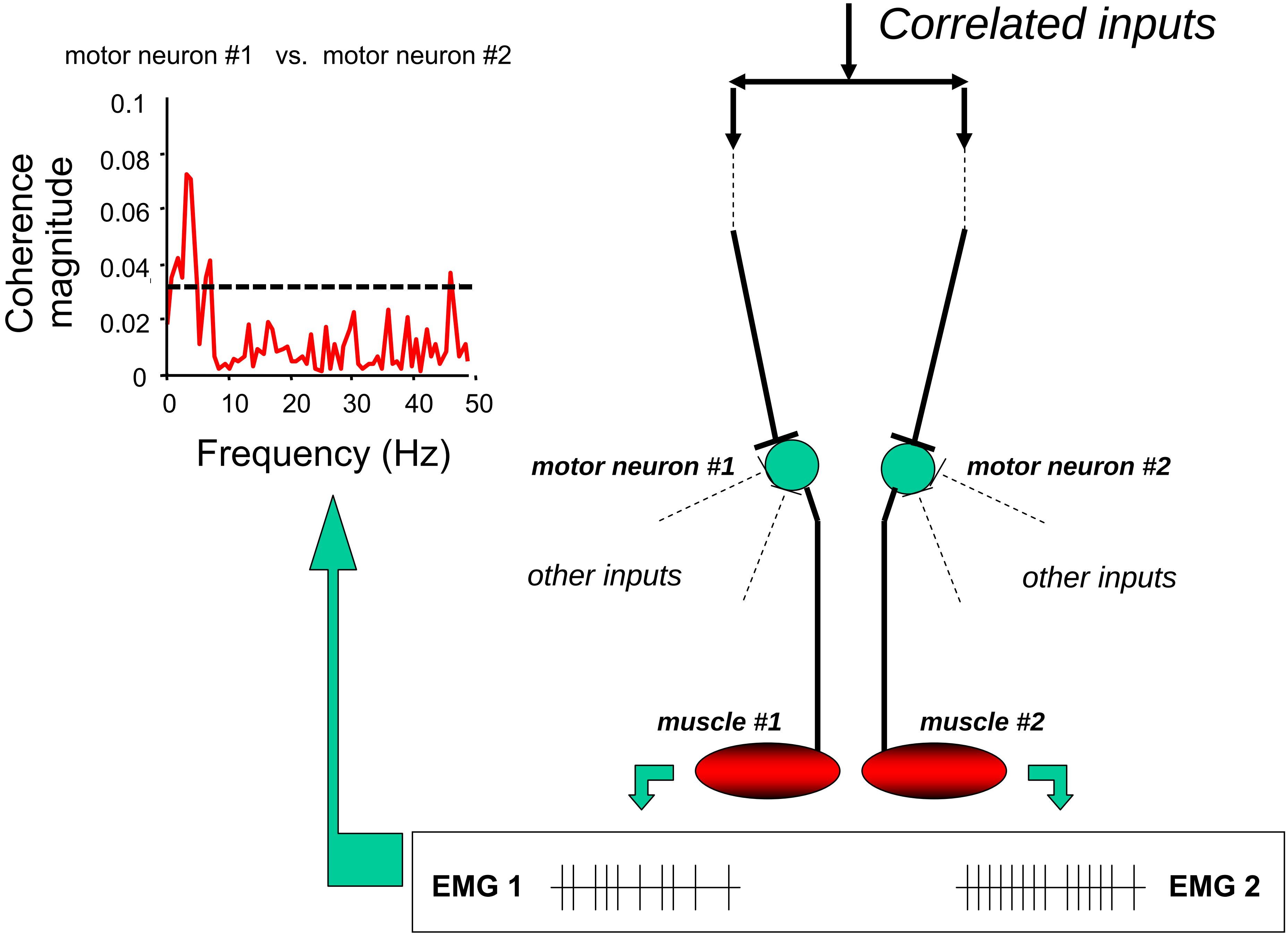
$$|R_{xy}(\lambda)|^2 = |f_{xy}(\lambda)|^2 / (f_{xx}(\lambda)f_{yy}(\lambda))$$

f_{xy} : cross-spectrum

f_{xx} , f_{yy} : auto-spectra

$$sig(\alpha) = 1-(1-\alpha)^{1/(L-1)}$$

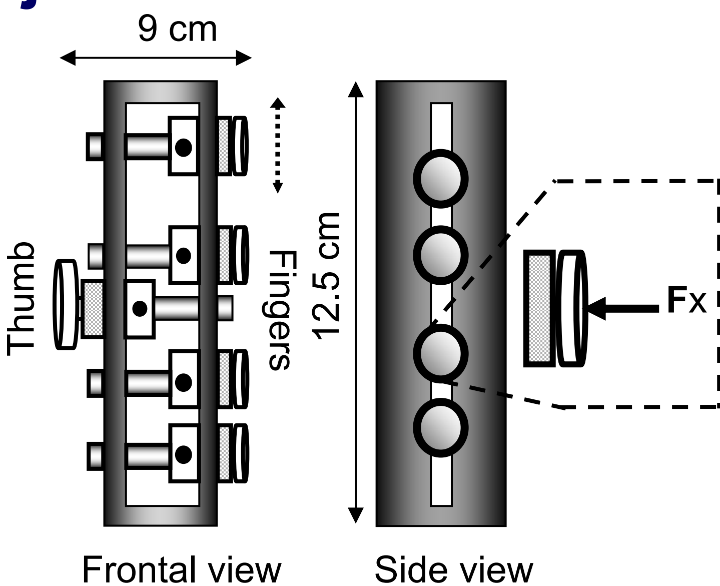
Coherence is a measure used to determine the linear relation between two signals in the frequency domain. Similar to the coefficient of determination (r^2) in linear statistics, the magnitude of coherence at a given frequency is bounded by 0 and 1, indicating that no linear relationship and a perfect linear relationship, respectively, exists at that frequency.

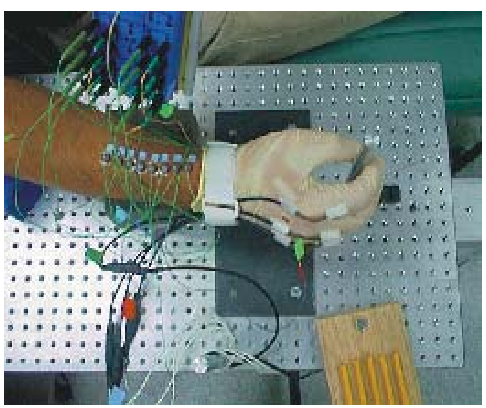


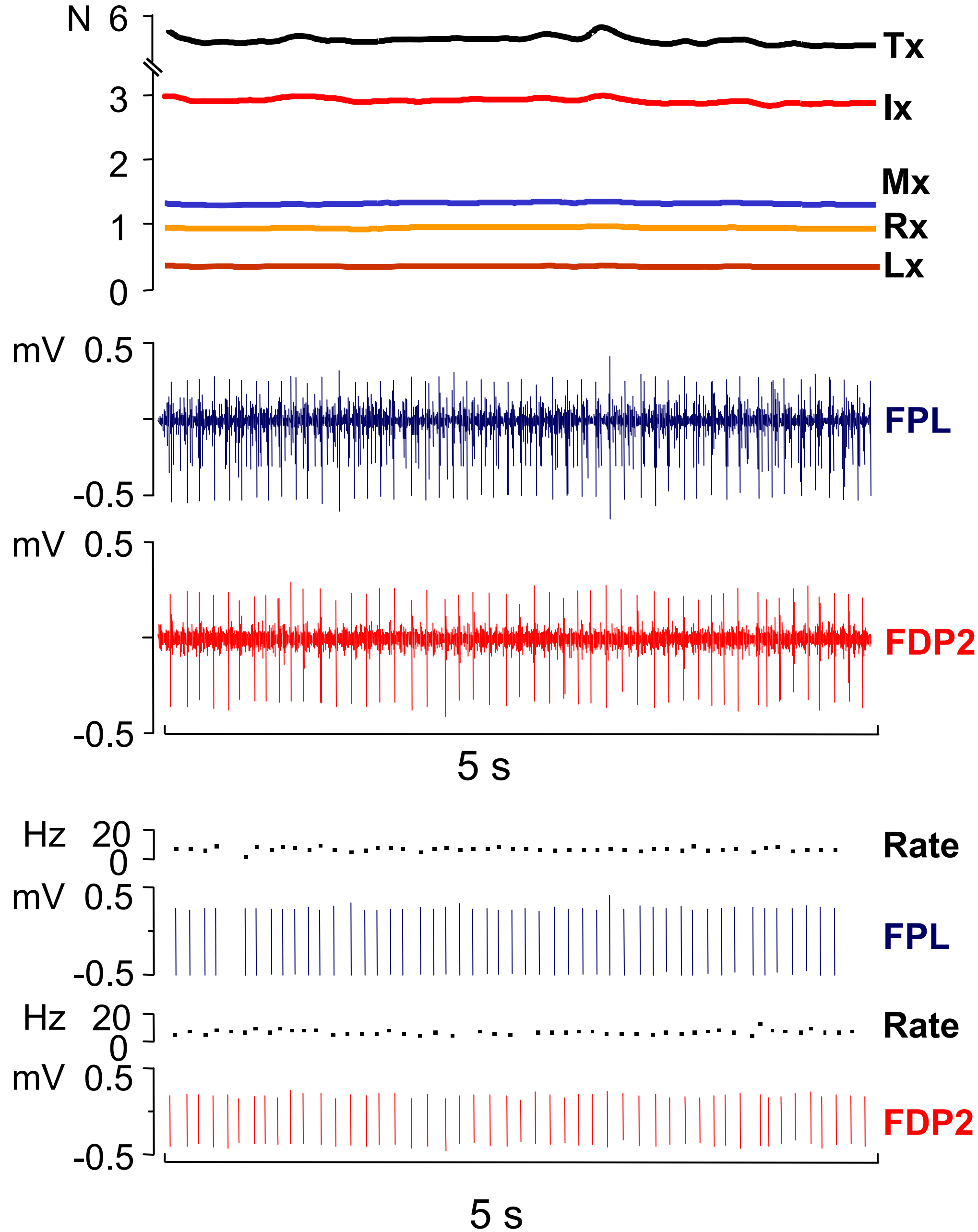
Correlated inputs
motor neuron #1 vs. motor neuron #2
Coherence magnitude
0.1
0.08
0.06
0.04
0.02
0
0
10
20
30
40
50
Frequency (Hz)
motor neuron #1
motor neuron #2
other inputs
other inputs
muscle #1
muscle #2
EMG 1
EMG 2

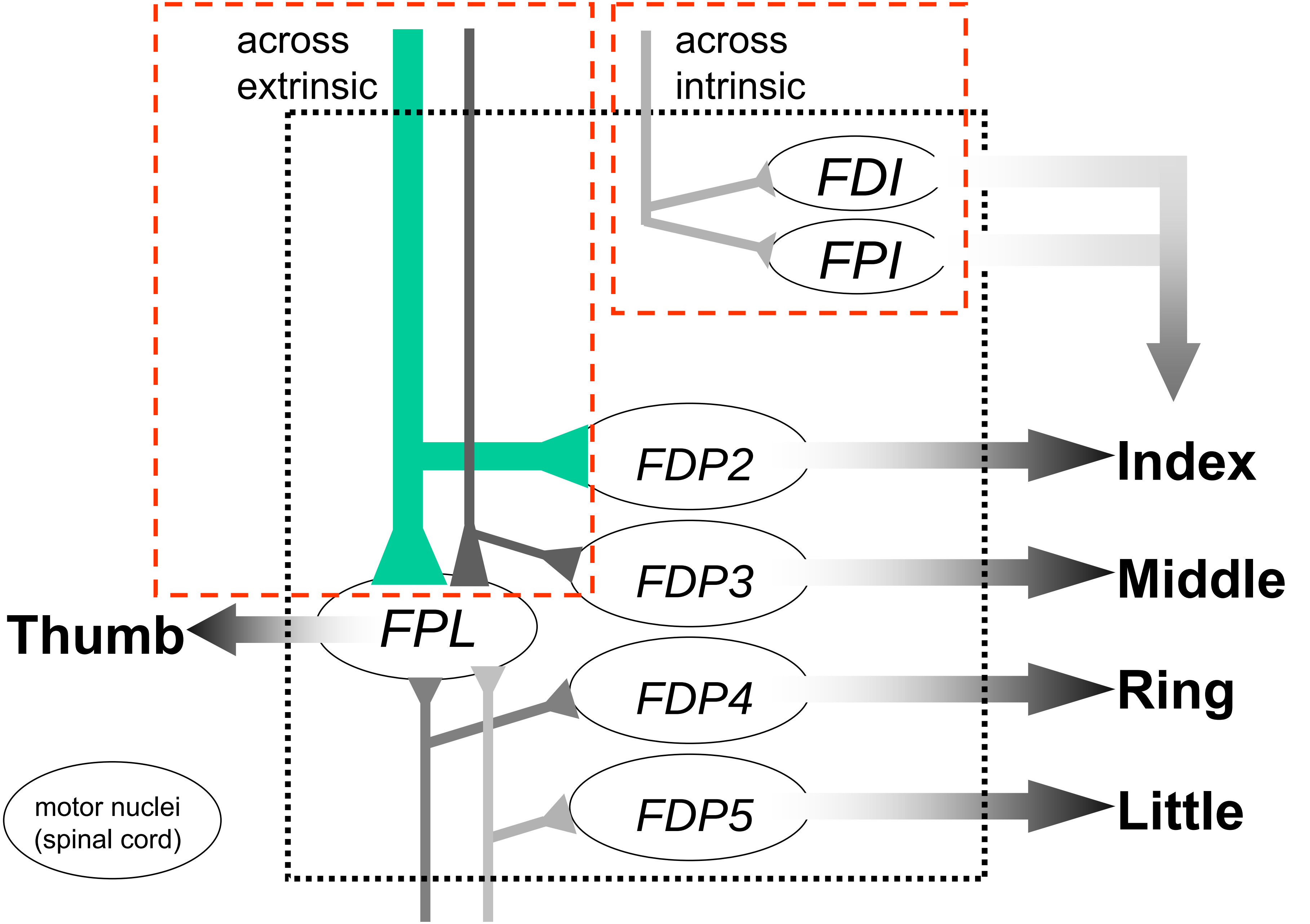
FIVE-DIGIT GRASPING

Single motor unit activity of extrinsic finger flexors during **object hold**



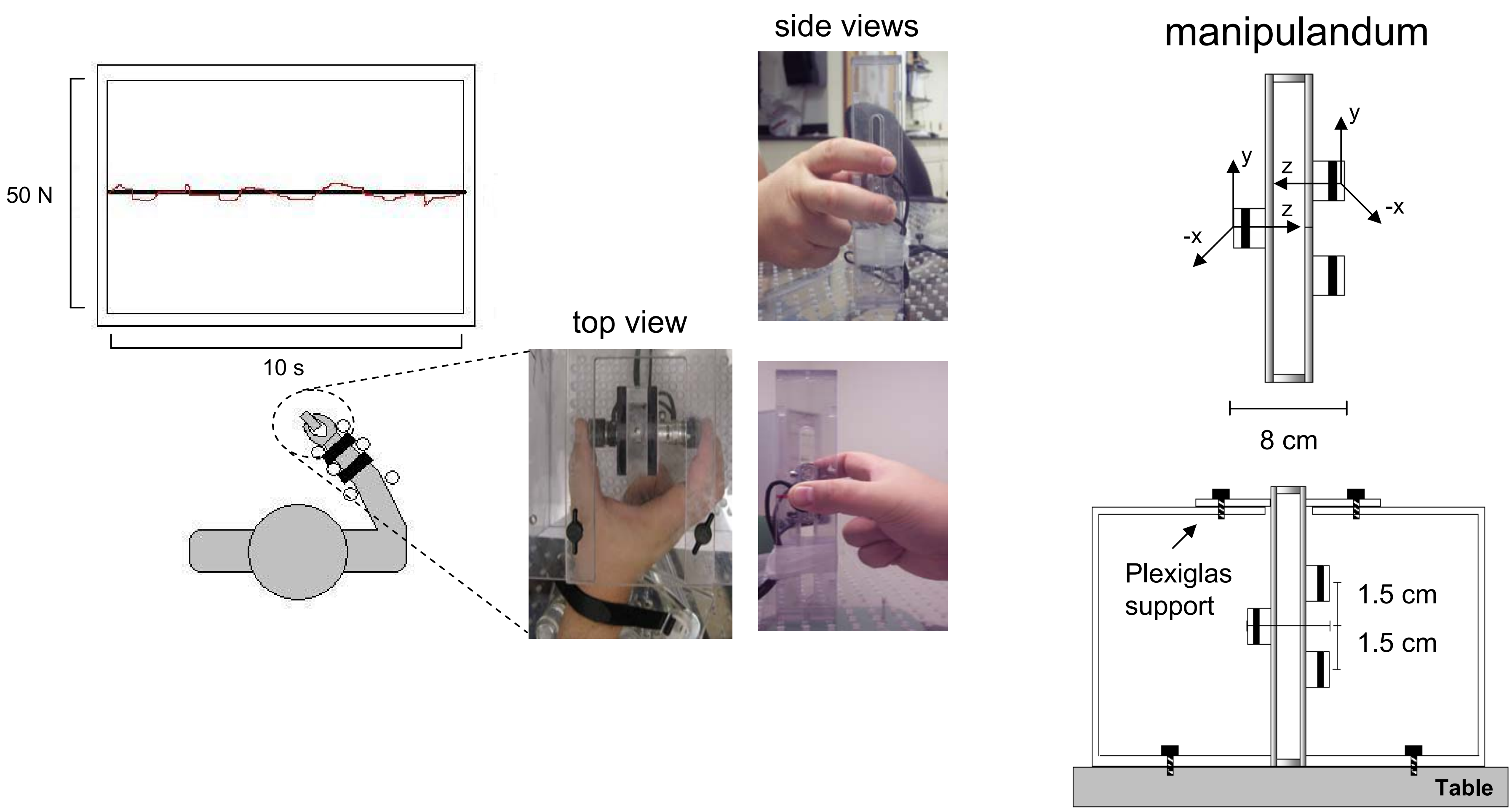




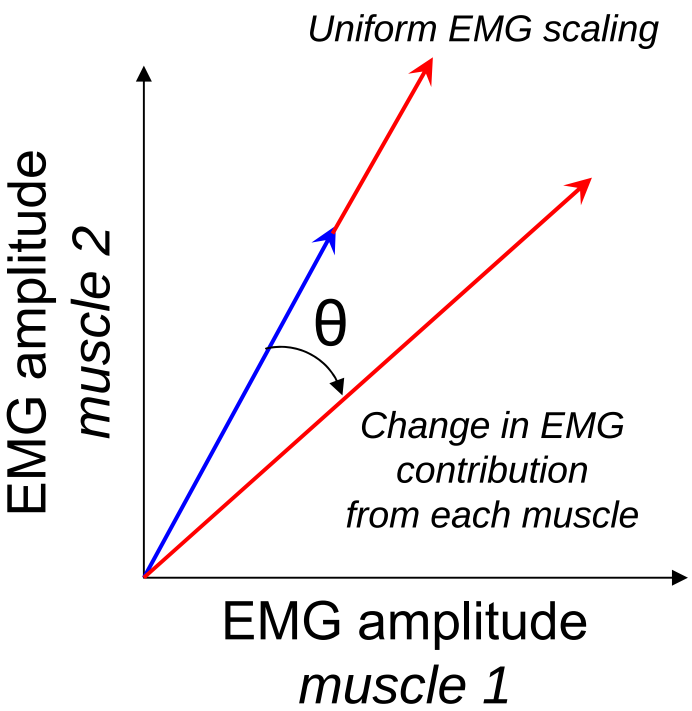


Winges and Santello (2004); Johnston et al. (2005); Winges et al. (2006, 2008)

Effect of force on coordination of multiple hand muscles



Vectorial representation and analysis of muscle activation patterns



MAP vector

$$\begin{bmatrix} \text{FDI EMG} \\ \text{FPI EMG} \\ \text{2DI EMG} \\ \vdots \\ \text{FPL EMG} \end{bmatrix}$$

MAP vector magnitude

$\mathrm{Sqrt}(\Sigma(x_1^2, x_2^2 \ldots x_n^2))$

MAP vector **5% MVC**

$$\begin{bmatrix} \text{FDI EMG} \\ \text{FPI EMG} \\ \text{2DI EMG} \\ \vdots \\ \text{FPL EMG} \end{bmatrix}$$

MAP vector **80% MVC**

$$\begin{bmatrix} \text{FDI EMG} \\ \text{FPI EMG} \\ \text{2DI EMG} \\ \vdots \\ \text{FPL EMG} \end{bmatrix}$$

Similarity b/w MAP vectors

$\cos(\theta)$

When $\cos(\theta) = 1$, uniform EMG scaling

EMG-EMG coherence analysis

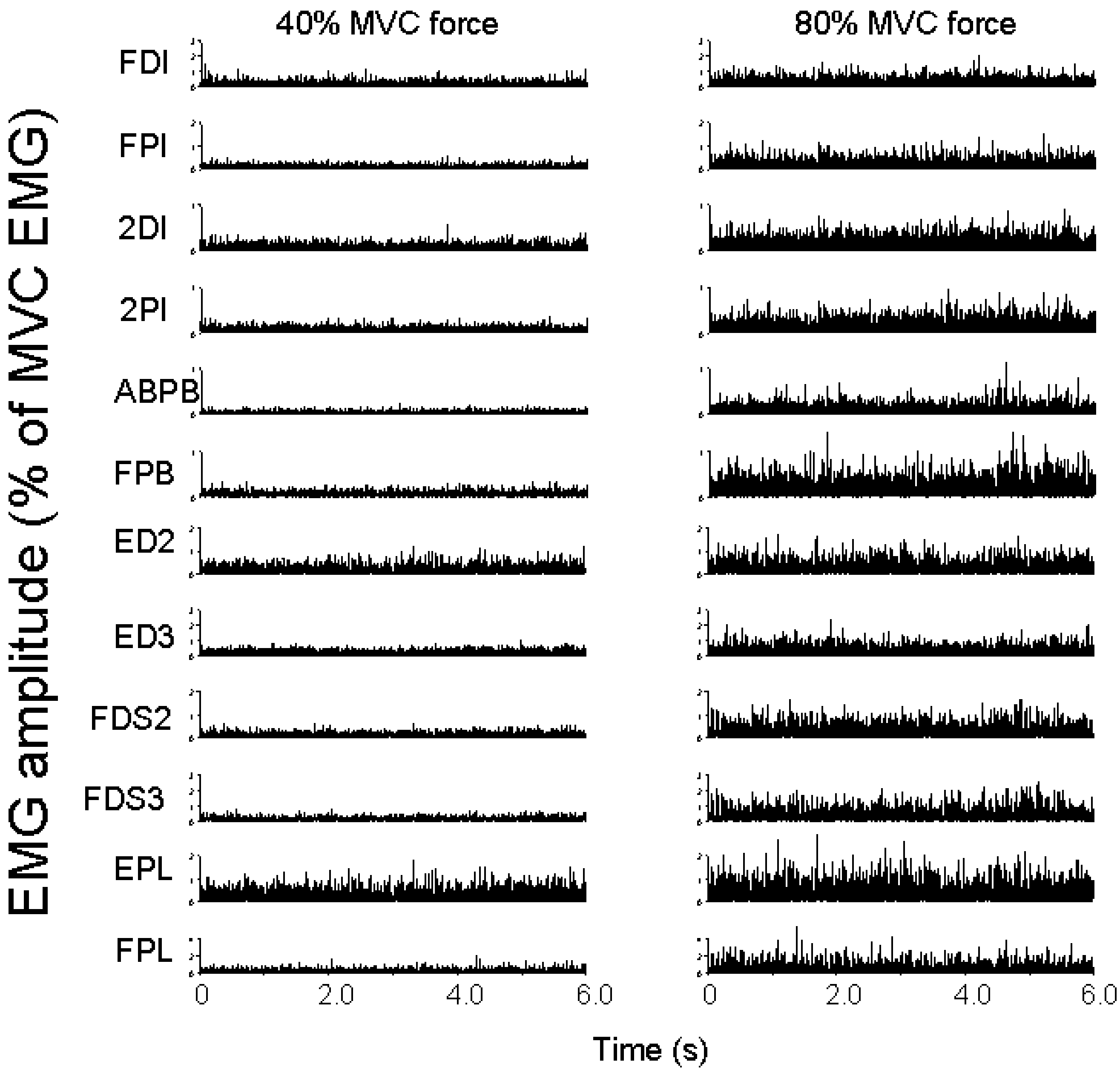
Twelve EMG signals results in 66 muscle pair combinations. We performed coherence analyses on:

- all 66 muscle pairs combined
  - across the entire frequency spectrum (0-55 Hz)
  - at separate frequency bands (0-5, 6-15, 16-35, 36-55 Hz), each band being associated with specific neural mechanisms (Brown, 2000).

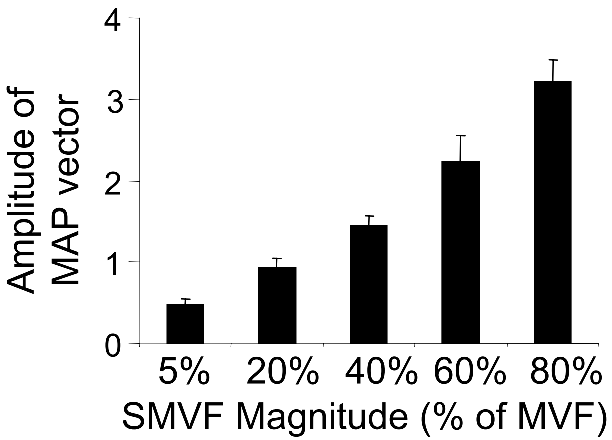
- on three sub-groups of muscle pairs (*extrinsic-extrinsic, intrinsic-intrinsic, intrinsic-extrinsic*)

Computation of EMG-EMG coherence was performed on un-rectified EMG that passed the stationarity test (>94% of the data) by using non-overlapping data segments at a frequency bin resolution of 1 Hz.

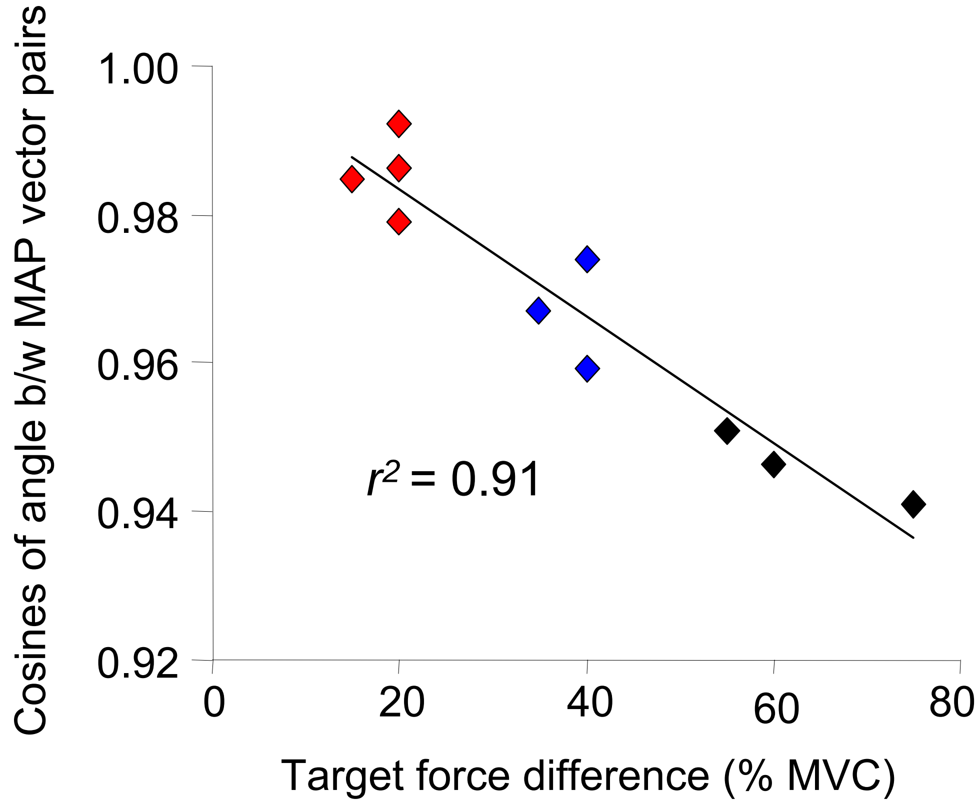
EMG as a function of force



The MAP vector length increased with force



The degree of similarity between MAP vectors depended on the proximity between target forces. Nevertheless, a strong similarity between vectors was found throughout the entire force range ($r > 0.94$).

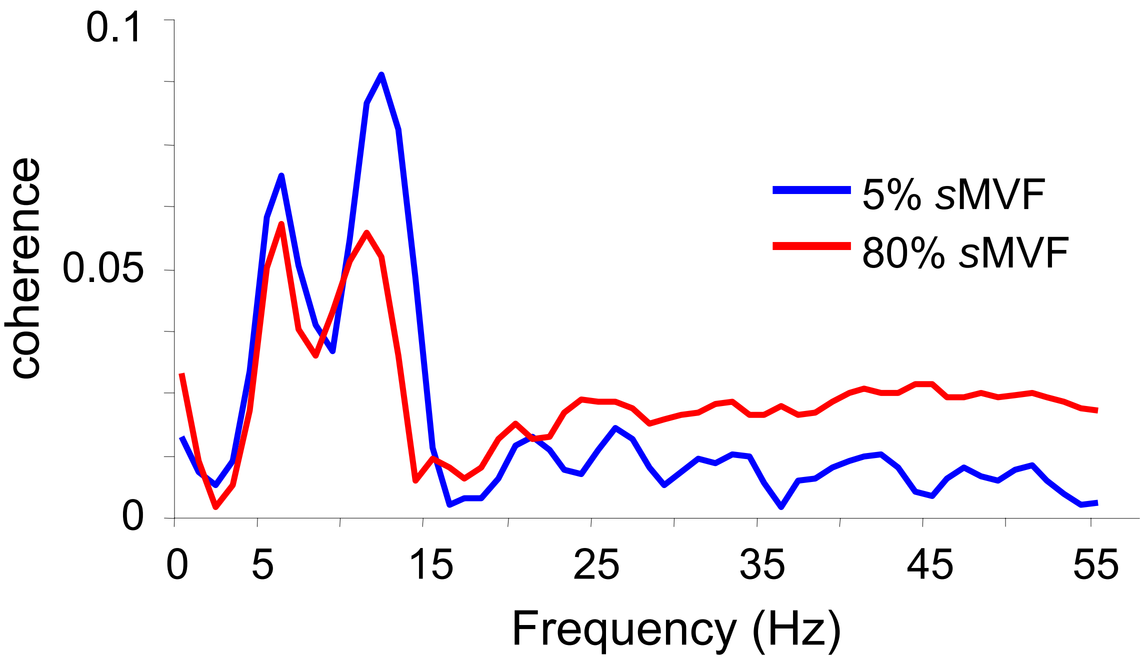


Comparison	SMVFs
C1	**5% vs 20%**
C2	**5% vs 40%**
C3	**5% vs 60%**
C4	**5% vs 80%**
C5	**20% vs 40%**
C6	**20% vs 60%**
C7	**20% vs 80%**
C8	**40% vs 60%**
C9	**40% vs 80%**
C10	**60% vs 80%**

C10 > C9, C7, C6, C5, C4, C3, C2
C8, C1 > C7, C6, C4, C3
C5 > C7, C4

All $p < 0.05$

Pooled coherence as a function of force (66 muscle pairs)



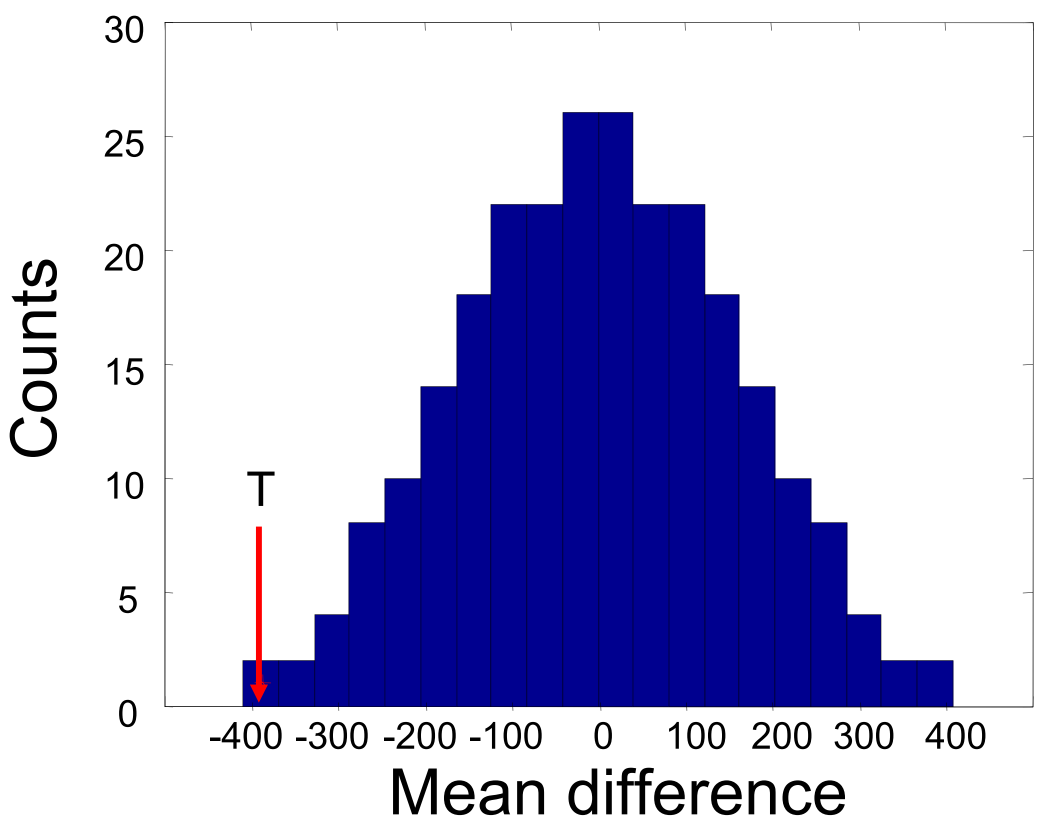
Integrals of coherence

	5%	**80%**
Sub #1	I*coh* (1,5)	I*coh* (1,80)
Sub #2	I*coh* (2,5)	I*coh* (2,80)
…	…	…
Sub #8	I*coh* (8,5)	I*coh* (8,80)

Amjad et al. (1997)

Non parametric statistical analysis of EMG-EMG coherence

	Initial values		Permutation #1		Permutation #2		Permutation #256	
	vector 1	vector 2	vector 1	vector 2	vector 1	vector 2	vector 1	vector 2
s1	**802.30**	294.40	294.40	**802.30**	**802.30**	294.40	294.40	**802.30**
s2	**784.73**	103.10	**784.73**	103.10	103.10	**784.73**	103.10	**784.73**
s3	**667.40**	168.00	168.00	**667.40**	**667.40**	168.00	168.00	**667.40**
s4	**671.00**	315.80	**671.00**	315.80	**671.00**	315.80	315.80	**671.00**
s5	**511.40**	182.70	182.70	**511.40**	**511.40**	182.70	182.70	**511.40**
s6	**699.60**	119.80	**699.60**	119.80	**699.60**	119.80	119.80	**699.60**
s7	**388.10**	163.10	163.10	**388.10**	163.10	**388.10**	163.10	**388.10**
s8	**321.40**	410.40	**321.40**	410.40	**321.40**	410.40	410.40	**321.40**
mean difference	**T = –386.08**		***x_1= 4.17***		***x_2= -159.42***		***x_{256}= 386.08***	

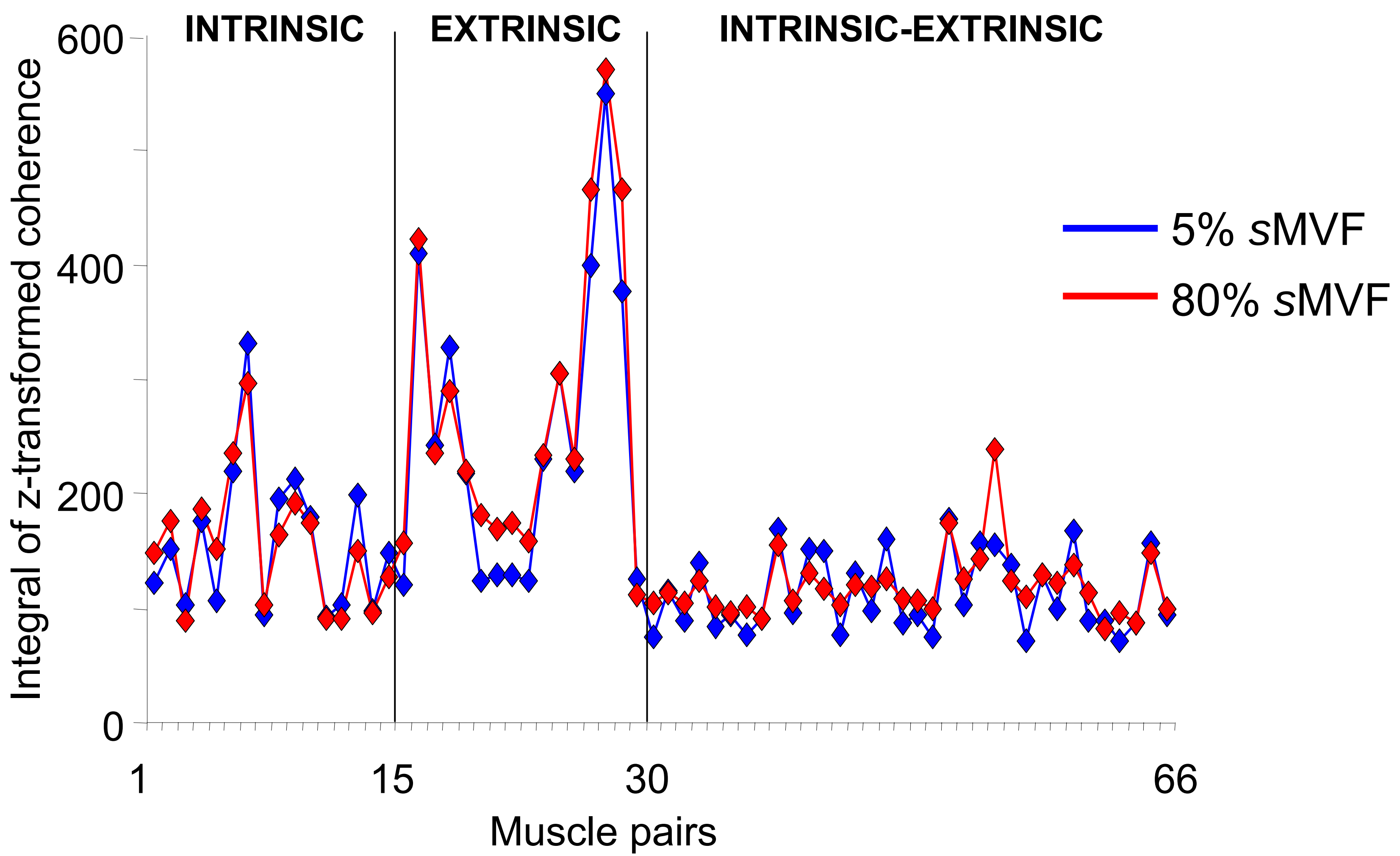


$$P = \frac{\textit{number of mean values} <= T}{\textit{number of permutations}}$$

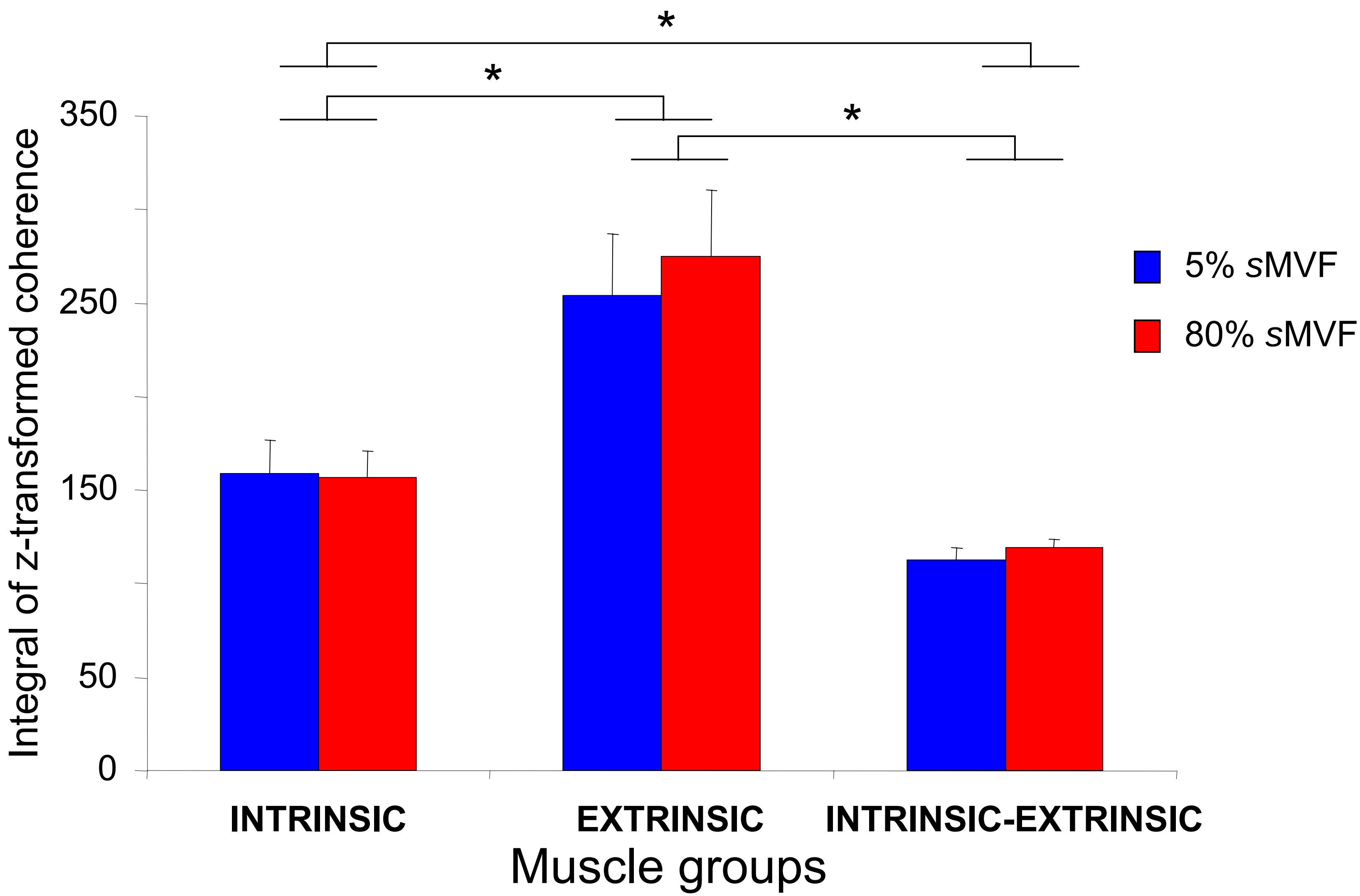
P = 9/256 = 0.0352

Nichols and Holmes (2001)

EMG-EMG coherence from each muscle pair (5% vs. 80% MVC).



Coherence pooled across *all* muscle pairs (66) or within *each muscle group* (3) was not significantly different between 5 and 80% MVC. However, *extrinsic muscle pairs* exhibited significantly **stronger coherence** than intrinsic and intrinsic-extrinsic muscle pairs.



Conclusions

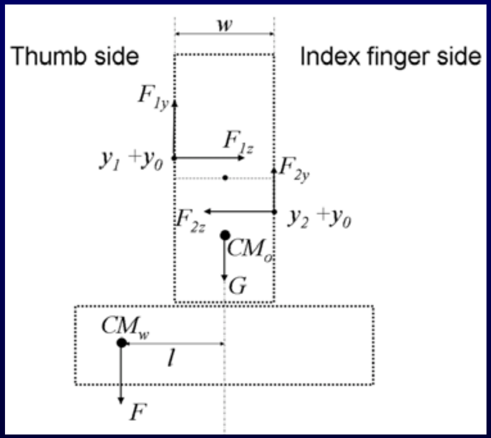
• The results of our EMG amplitude analyses extend and confirm previous work on single digit force production tasks by revealing a **high degree of similarity in EMG coordination pattern vectors across a wide range of sub-maximal forces.**

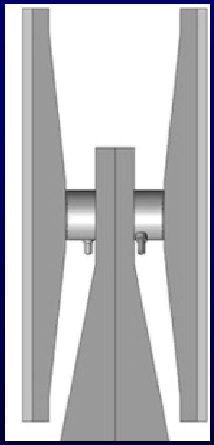
• The results of EMG-EMG coherence are consistent with the results of EMG amplitude analyses by showing that **the strength of correlated input to multiple hand muscles is invariant across force levels.**

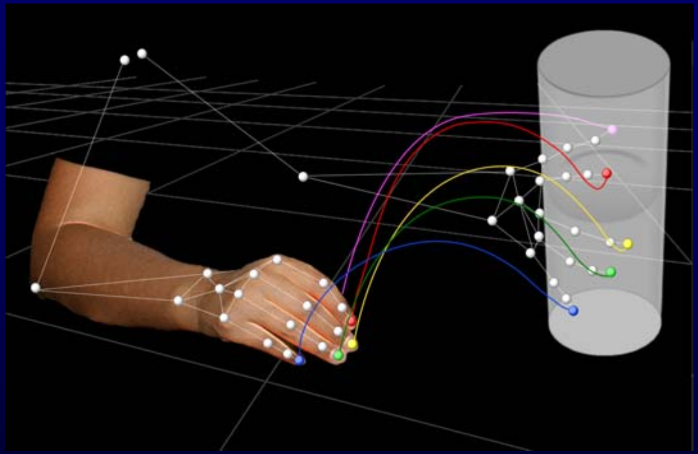
Together, these findings point to a force-independent mechanism responsible for coordinating the simultaneous activity of multiple hand muscles.

- Although the strength of correlated input to hand muscles remained constant across force levels, **its distribution was heterogenous as indicated by the strongest correlation among extrinsic muscle pairs.**

- These results are consistent with – and extend - the results we obtained from single motor unit studies recorded at ~5% MVC during object hold (Winges et al., 2004, 2008). As such, the present EMG-EMG coherence results further **point to a functional/anatomical gradient underlying the distribution of correlated neural input to motor nuclei of hand muscles.**







Learning Object Grasping and Manipulation

Anticipatory Grasp Control

Sensorimotor memories

Control of digit forces and positions

Background

The ability to anticipate object center of mass location allows to predict digit forces necessary to counteract the external torque on the object[1]. The results of two studies from our laboratory on anticipatory control of digit placement revealed that subjects

- implement anticipatory force control mechanisms *in parallel* with careful selection of digit placement[2]
- are able to use explicit cues about CM location for the modulation of digit placement but not forces, suggesting the existence of ***independent*** sensorimotor memories for these two variables[3]

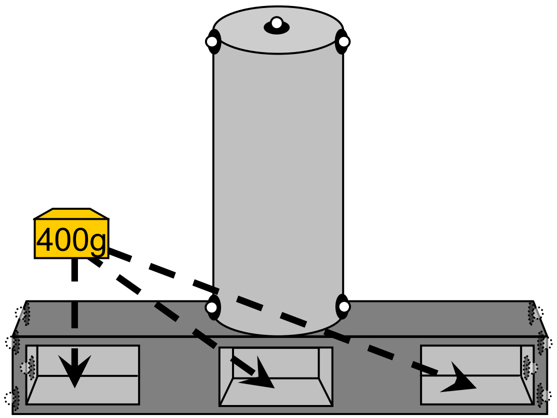
Caterina Ansuini

Jamie Lukos

[1] Salimi et al., Exp Br Res (2000, 2003);
[2] Lukos et al., J Neurosci (2007)
[3] Lukos et al., J Neurosci (2008)

Task

We asked subjects to reach, grasp, lift and replace with their right hand a T-shaped object. The center of mass of the object was changed either in a trial-to-trial fashion or across blocks of trials

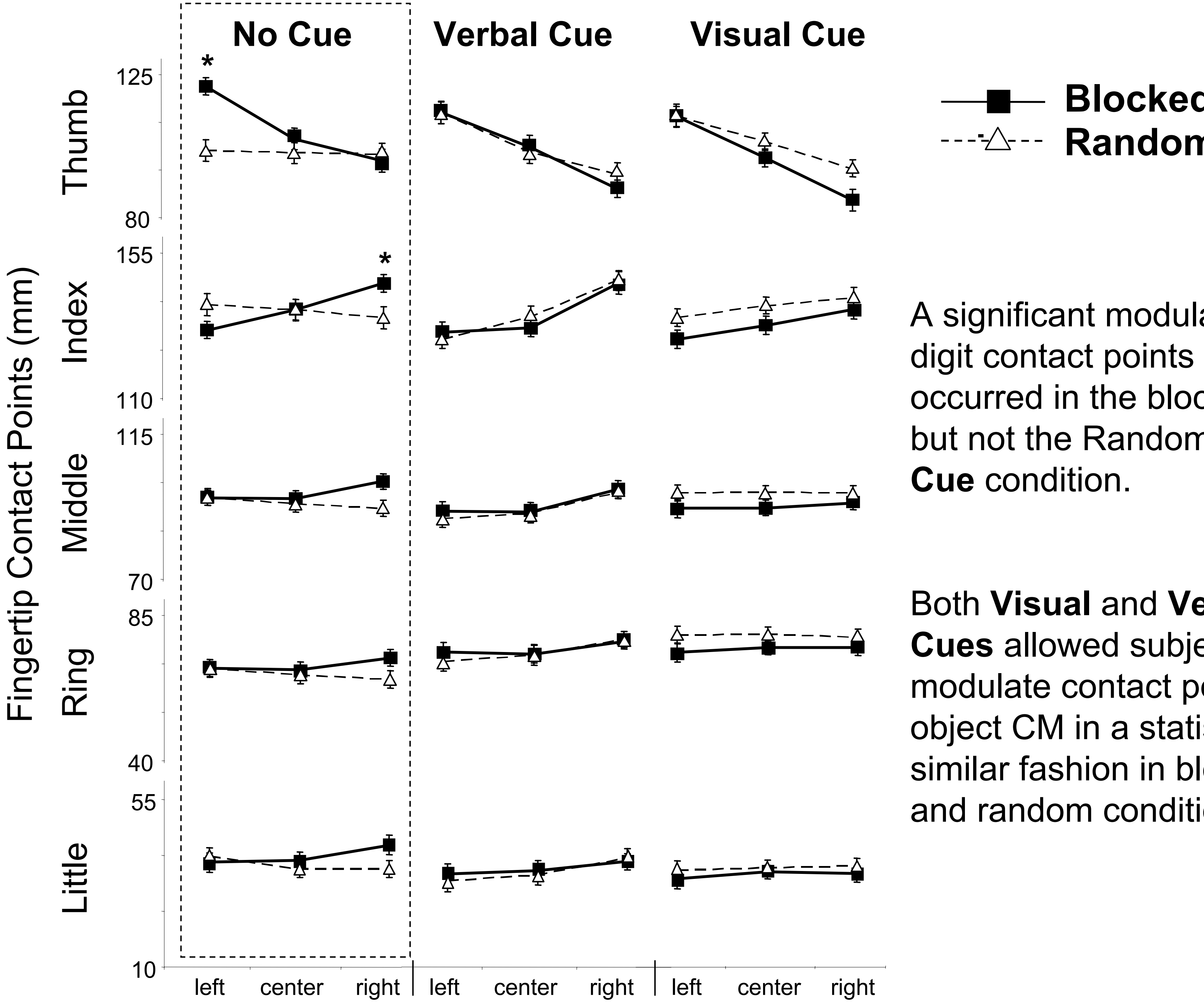


(predictable and unpredictable condition, respectively) by adding a mass in one of three slots at the base of the object.

The only task requirement was to minimize object roll during the lift.

We hypothesized that *a priori* knowledge of CM location would allow subject to predict the appropriate forces and distribution of digit placement to counteract the external torque.

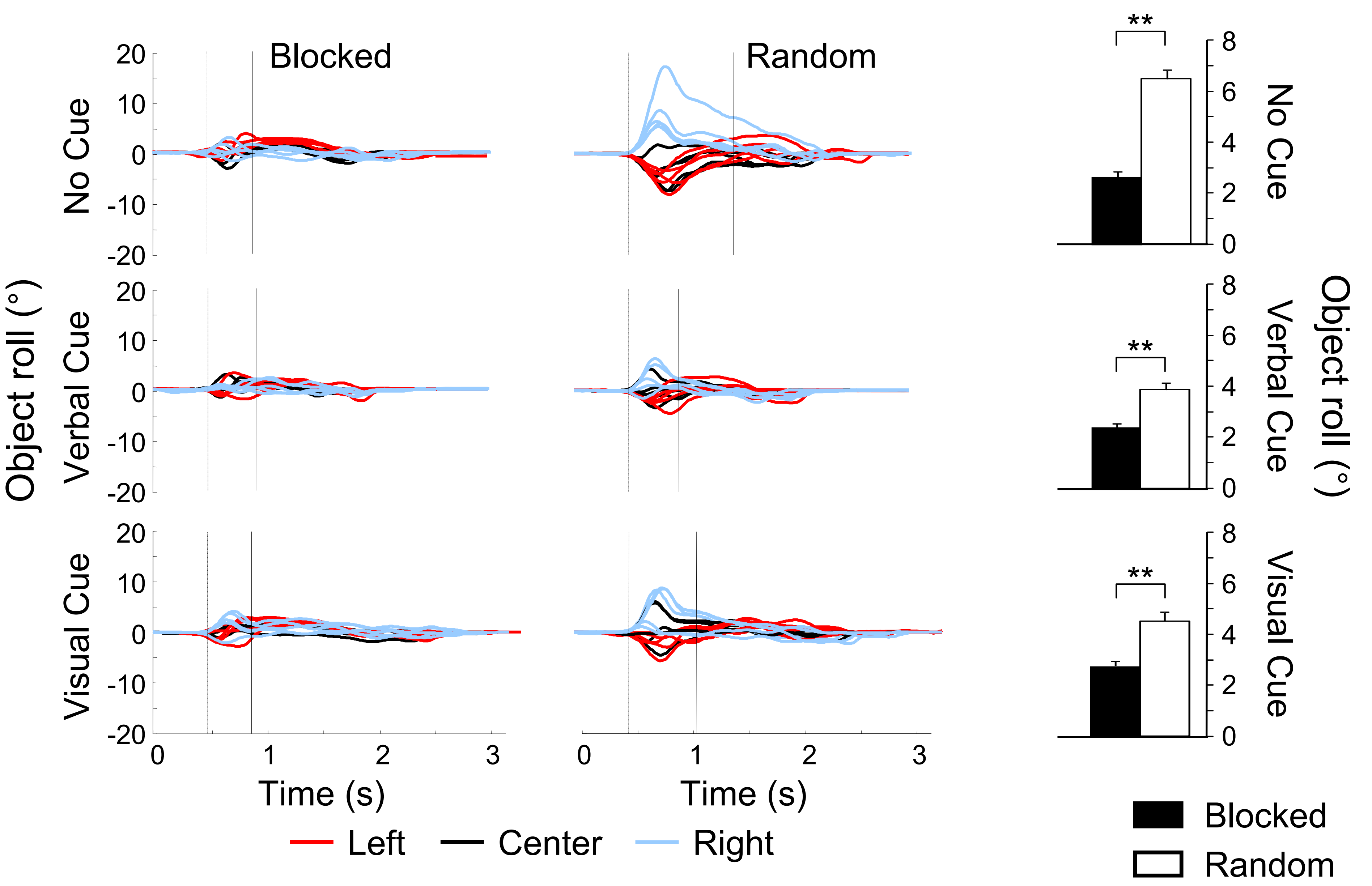
The unpredictable condition was used to determine the strategy that would be used when CM could not be anticipated.



A significant modulation of digit contact points occurred in the blocked, but not the Random **No Cue** condition.

Both **Visual** and **Verbal Cues** allowed subjects to modulate contact points to object CM in a statistically similar fashion in blocked and random conditions.

Cues did not allow subjects to minimize object roll in the random condition to the same extent as in the blocked condition ($p < 0.05$).



Conclusions (Background)

As subjects perform consecutive trials of object manipulation (procedural learning) they implement anticipatory force mechanisms *in parallel* with careful selection of digit placement (Lukos et al., 2007).

In contrast, a *differential effect* on anticipatory control of grasp kinematics vs. kinetics was found when subjects were provided with arbitrary cues about object CM location.

Consistent with work on two-digit grasping (Turrell et al. 1999; Flanagan and Beltzner 2000; Salimi et al. 2003), our data suggests that non-consecutive (random) practice of object manipulation **interferes** with the information provided by cues for retrieval of sensorimotor memories of ***digit forces***.

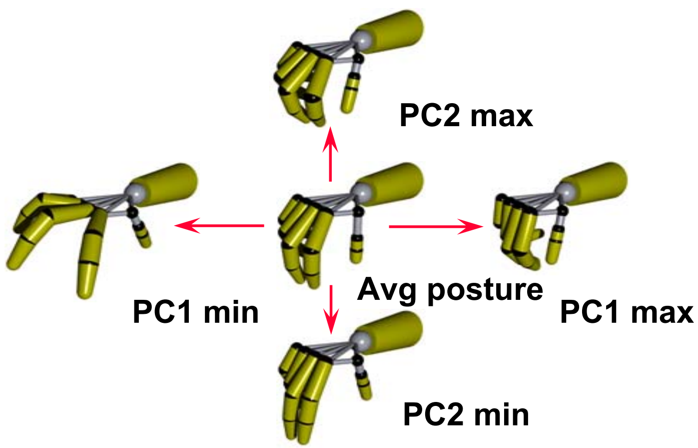
The effectiveness of cues in anticipating contact points in the random condition, however, indicates that sensorimotor memories of ***digit positions*** are ***not*** biased by having sensed a different object property in the previous trial.

Anticipatory Coordination of Grasp Positions and Forces for Dexterous Two-Digit Manipulation

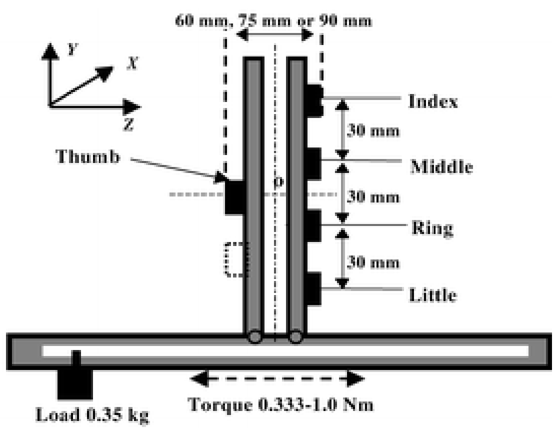
Qiushi Fu

Wei Zhang

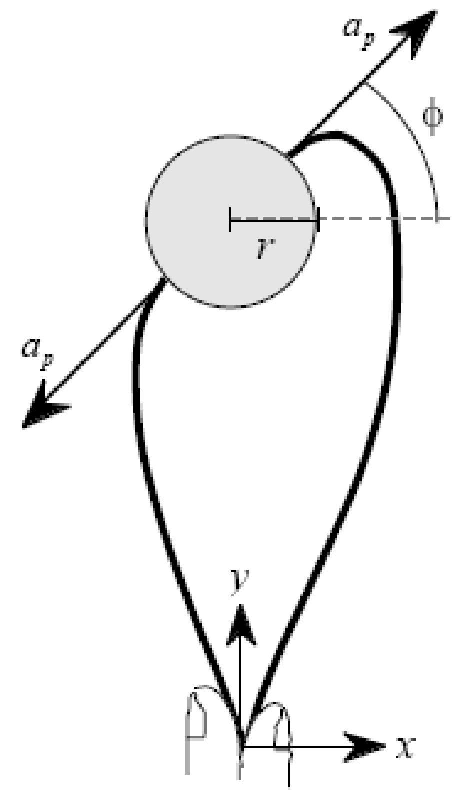
Dexterous object manipulation requires accurate anticipatory distributions of digit positions and forces. However, grasping studies have focused **either** on hand kinematics **or** kinetics. Therefore, **how humans learn to coordinate these two variables has not been studied**.



Santello, Flanders and Soechting, J Neurosci (1998)
Santello, Flanders and Soechting, J Neurosci (2002)

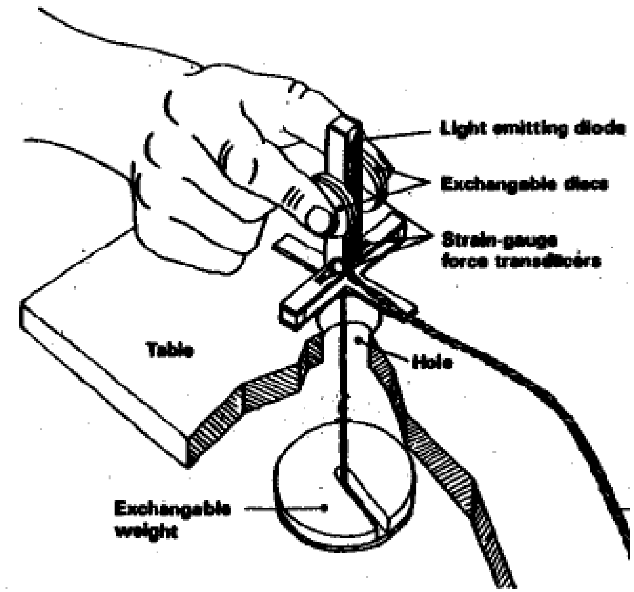


Latash and Zatsiorsky, Adv Med Exp Biol (2009)

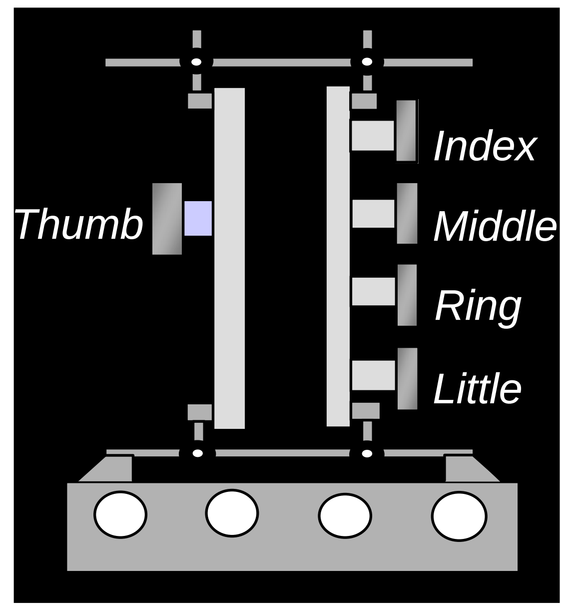


Smeets and Brenner, Motor Control (1999)

In experimental tasks that force digit placement on fixed locations on the object, subjects position their digits on the **same locations** on every trial and control digit forces in an anticipatory fashion by using sensorimotor memories from previous trials.



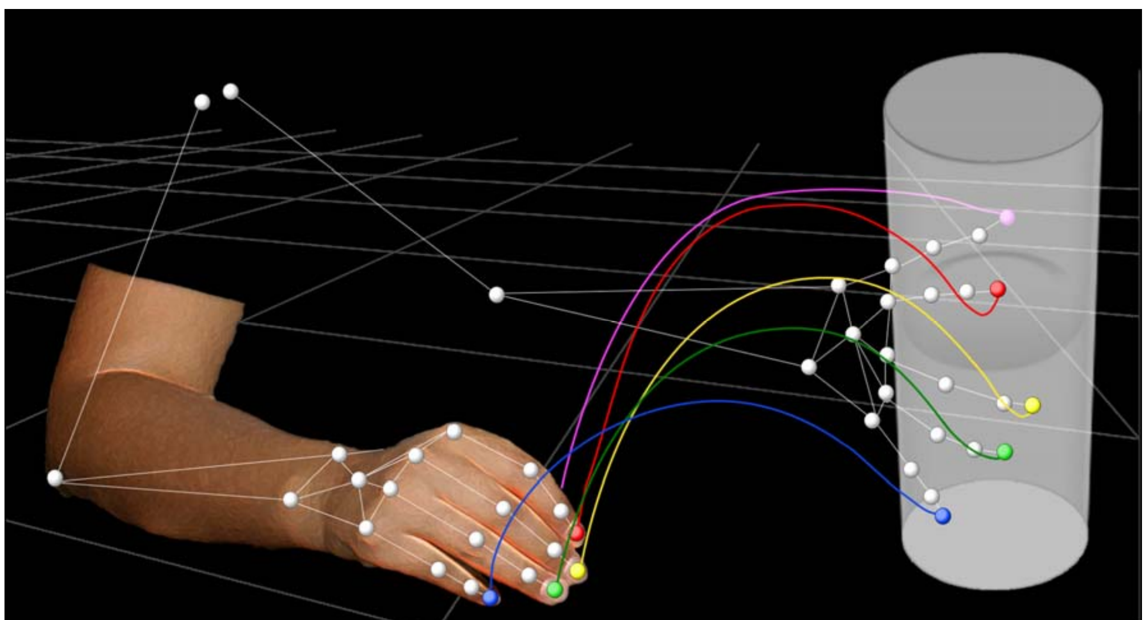
Westling and Johansson, Exp Br Res (1984)
Johansson and Flanagan, Nat Rev Neurosci (2009)



Rearick, Casares and Santello
J Neurophysiol (2002)

However, when digit position is not constrained by the experimenter, digit placement may vary from trial to trial due to variability in fingertip trajectories during the reach.

Therefore, the question arises as to whether learning of object manipulation is attained through **(a)** the accurate trial-to-trial reproduction of digit placement, **hence forces**, or **(b)** whether force modulation relies on the integration of sensorimotor memories and sensing of digit position.

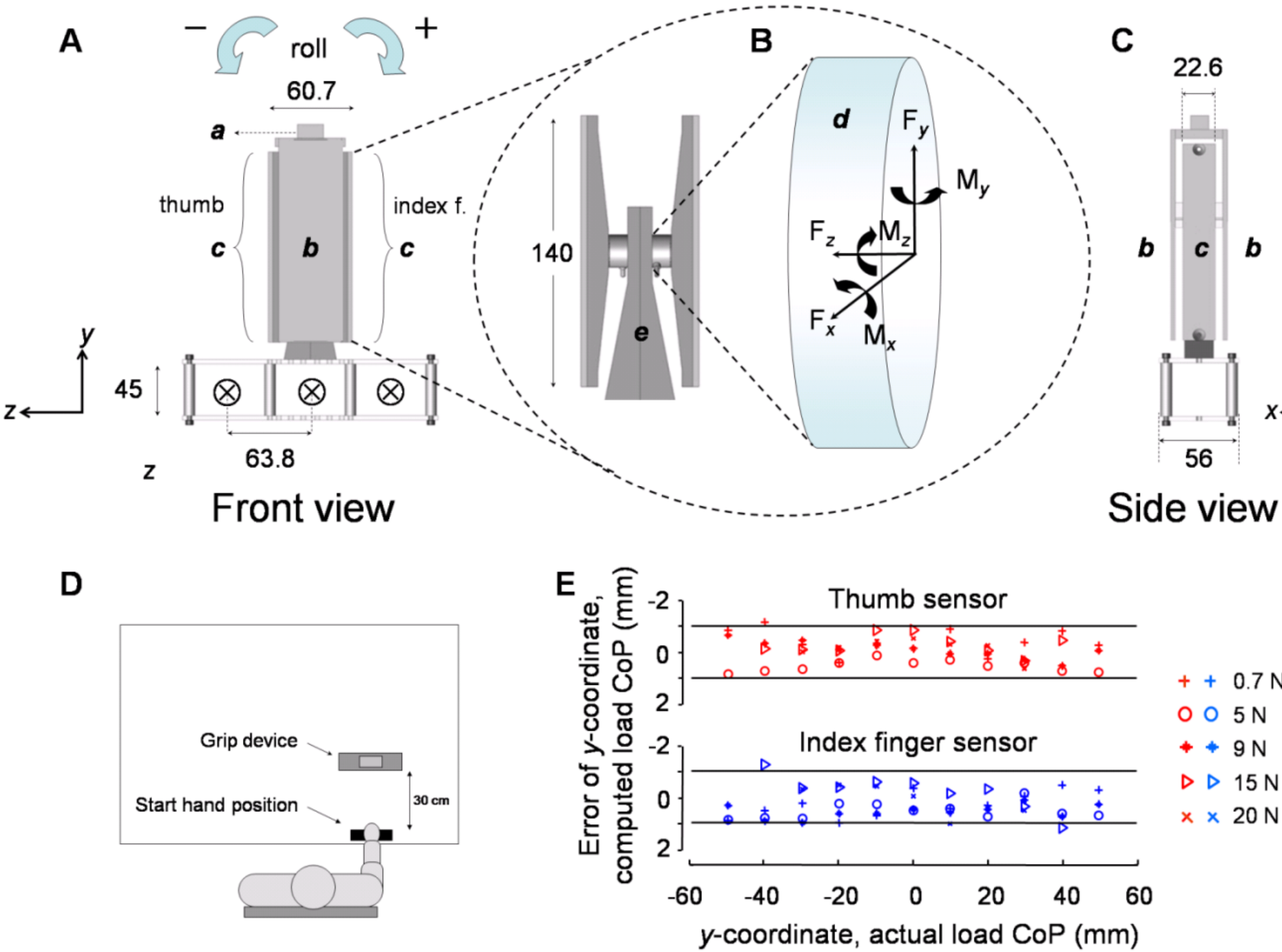


Experimental setup: Grip device (two-digit grasping)

We designed and built a device to

(a) measure **forces** and **torques** exerted by one digit on either side of the object, and

(b) compute the digit **center of pressure**.



A
B
C
roll
60.7
a
thumb
index f.
c
b
c
45
63.8
z
y
z
Front view
140
e
d
F_y
M_y
F_z
M_z
F_x
M_x
22.6
b
c
b
y
x
56
Side view
D
Grip device
Start hand position
30 cm
E
Thumb sensor
Index finger sensor
Error of y-coordinate, computed load CoP (mm)
y-coordinate, actual load CoP (mm)
-2
0
2
-60
-40
-20
0
20
40
60
0.7 N
5 N
9 N
15 N
20 N

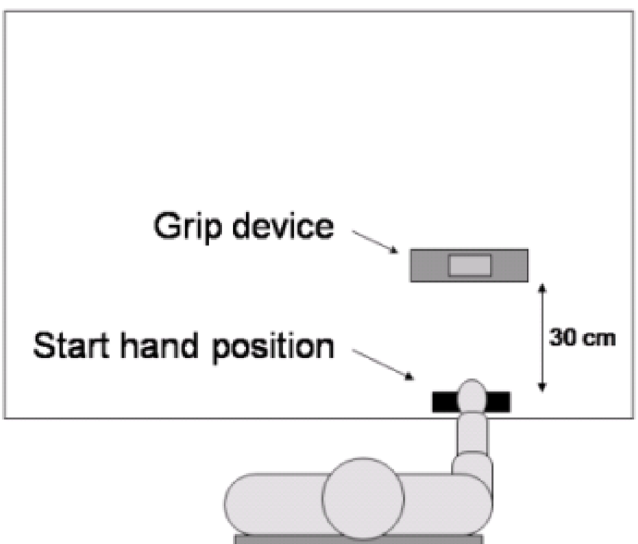
Experimental task

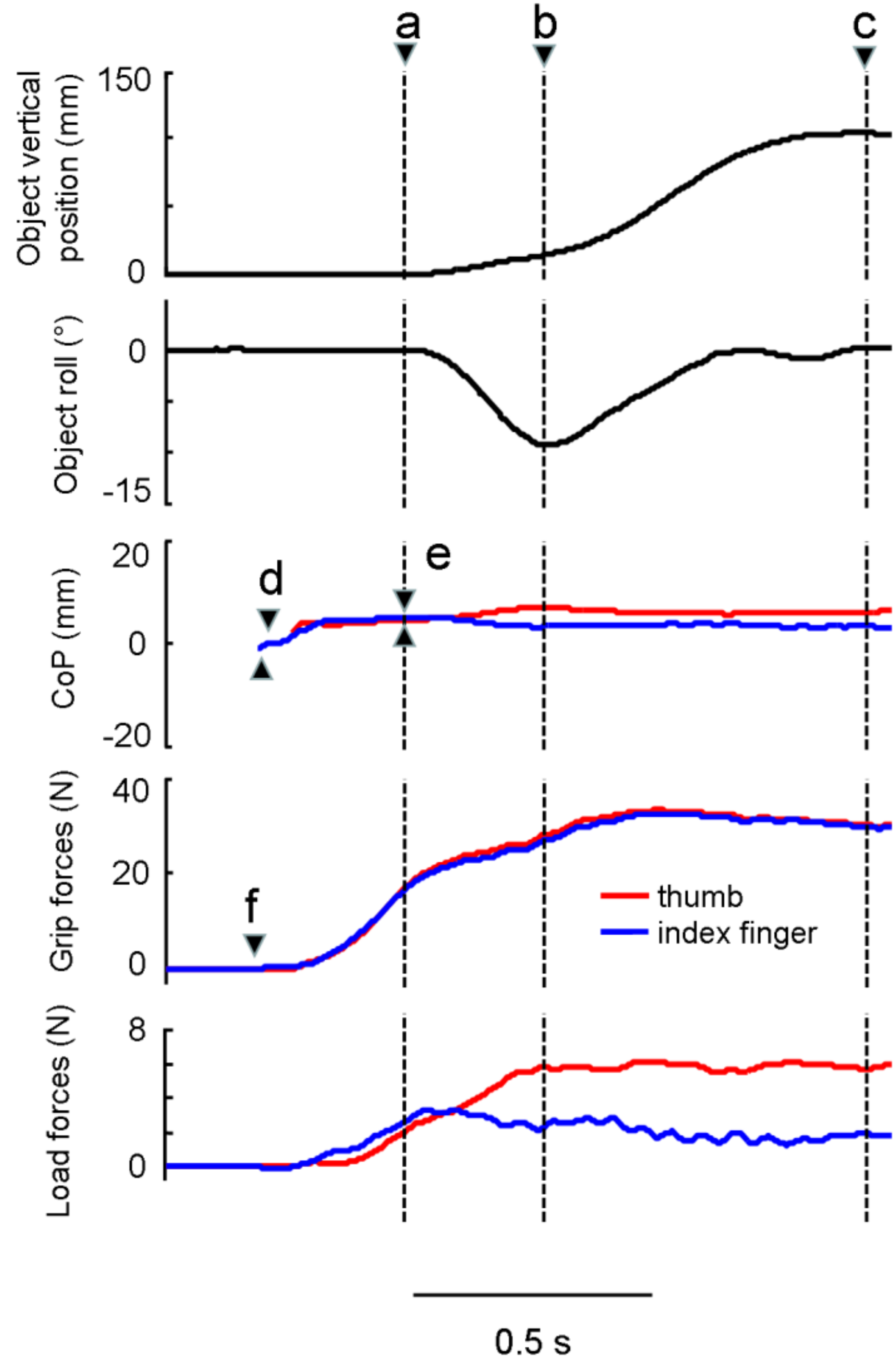
We asked subjects to:

• grasp the object with the **thumb** and **index finger**

• lift the object while preventing it from rolling

• hold the object and replace it





Experimental variables

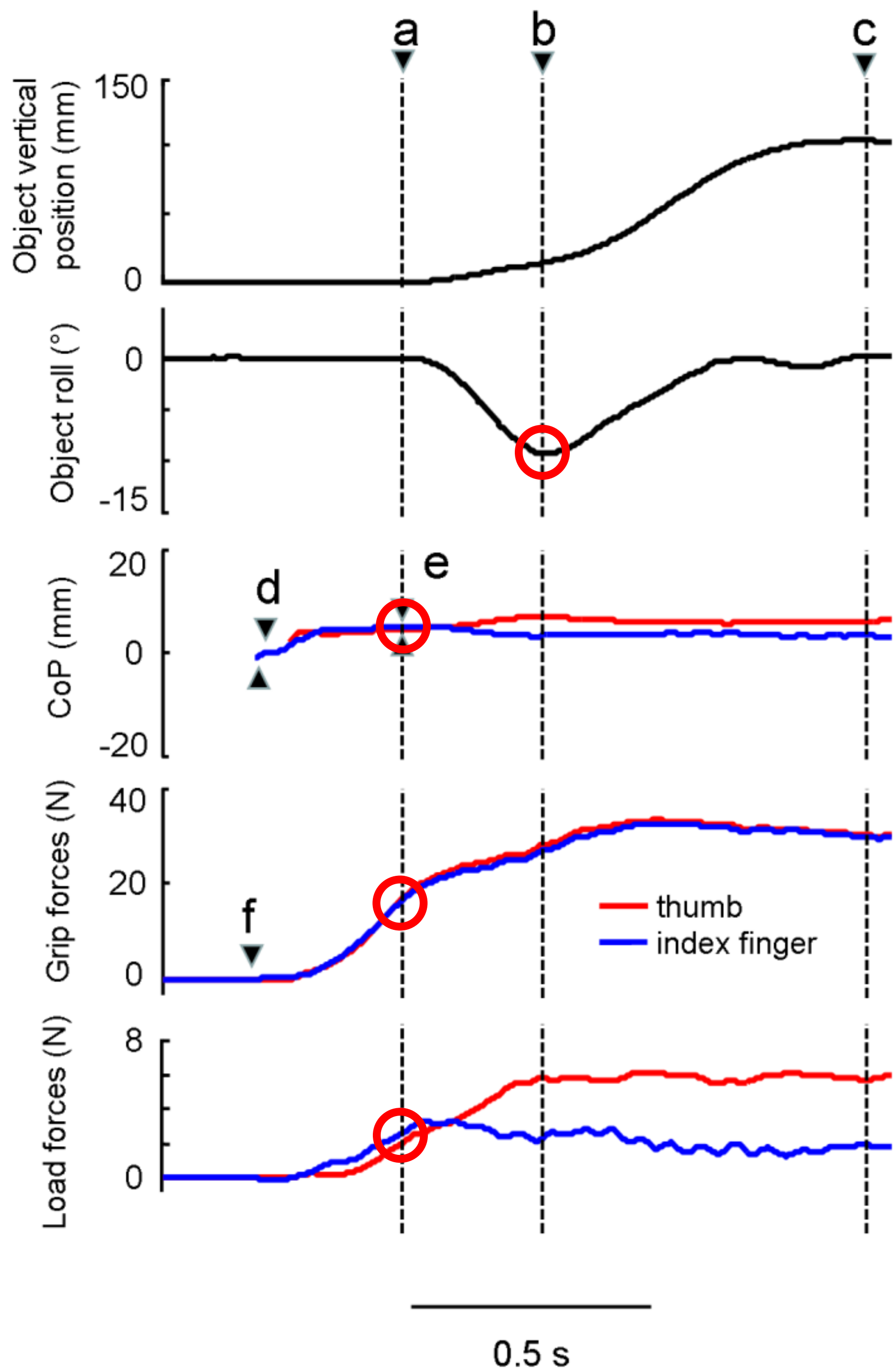
As we focused on the anticipatory component of grasp control, we analyzed the following variables **at the object lift onset (b)**:

• *normal and tangential forces* exerted by thumb and index finger

• thumb and index finger *center of pressure* (CoP)

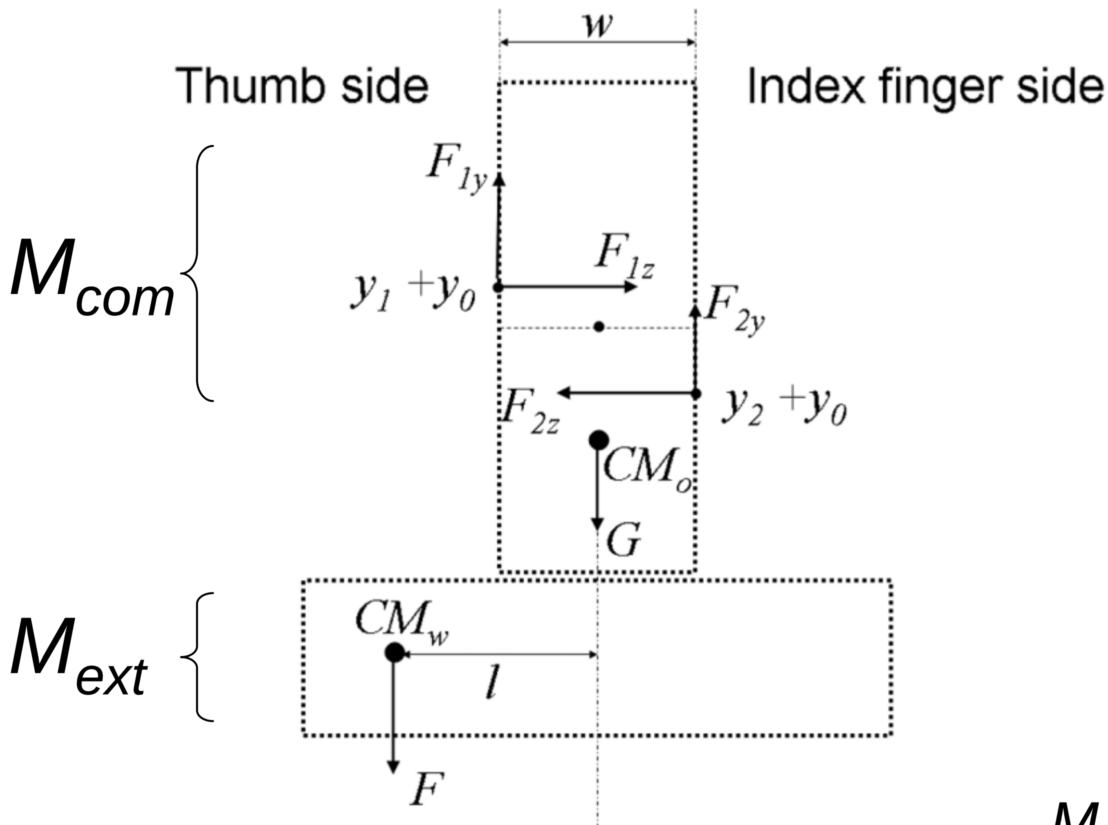
• *normal and tangential components* of the *digits' net moment*

To quantify performance, we also measured *peak object roll* during lift.



Task mechanics

Attainment of successful object roll minimization can be described as the subjects' ability to generate a compensatory moment (***M_{com}***) on the object **at object lift onset** that is of equal magnitude and opposite direction to that of the external moment (***M_{ext} = Fl***) caused by added mass about the center of mass of the unloaded object (*CM_w* and *CM_0*, respectively).

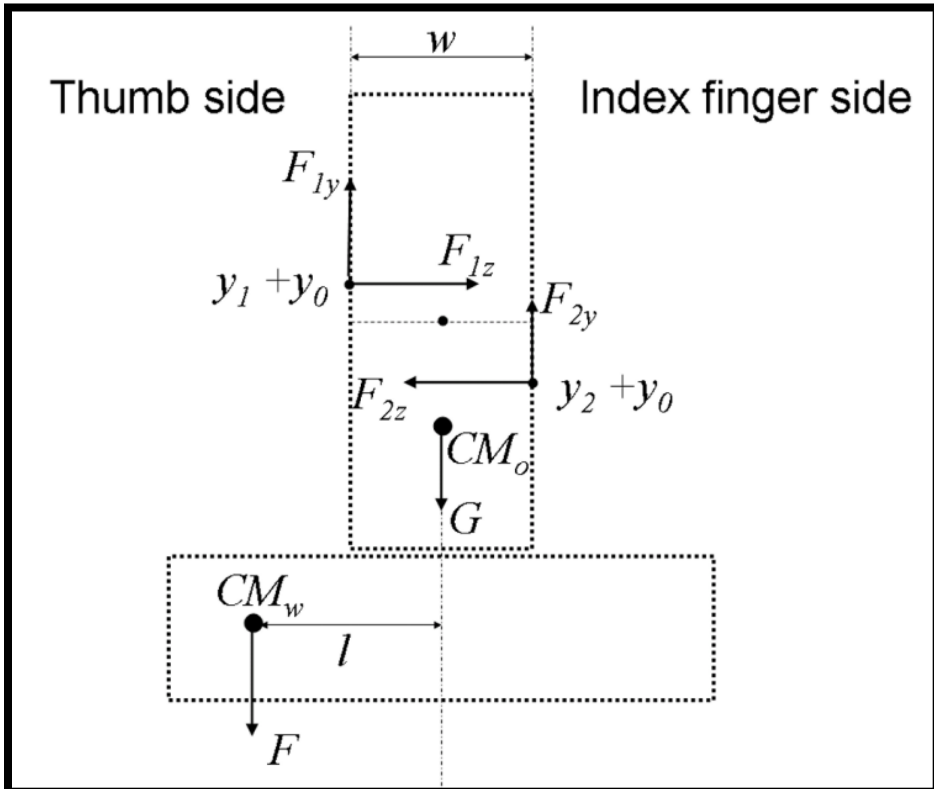


M_{ext} = ±255 Nmm

Perfect anticipation at object lift onset: $M_{com} = -M_{ext}$

$$M_{com} = \frac{w}{2}F_{1y} - \frac{w}{2}F_{2y} + (y_1 + y_0)F_{1z} - (y_2 + y_0)F_{2z} \quad (1)$$

F_{iy} = load force, F_{ix} = normal force
i = 1, thumb; 2, index finger



Perfect anticipation at object lift onset: $M_{com} = -M_{ext}$

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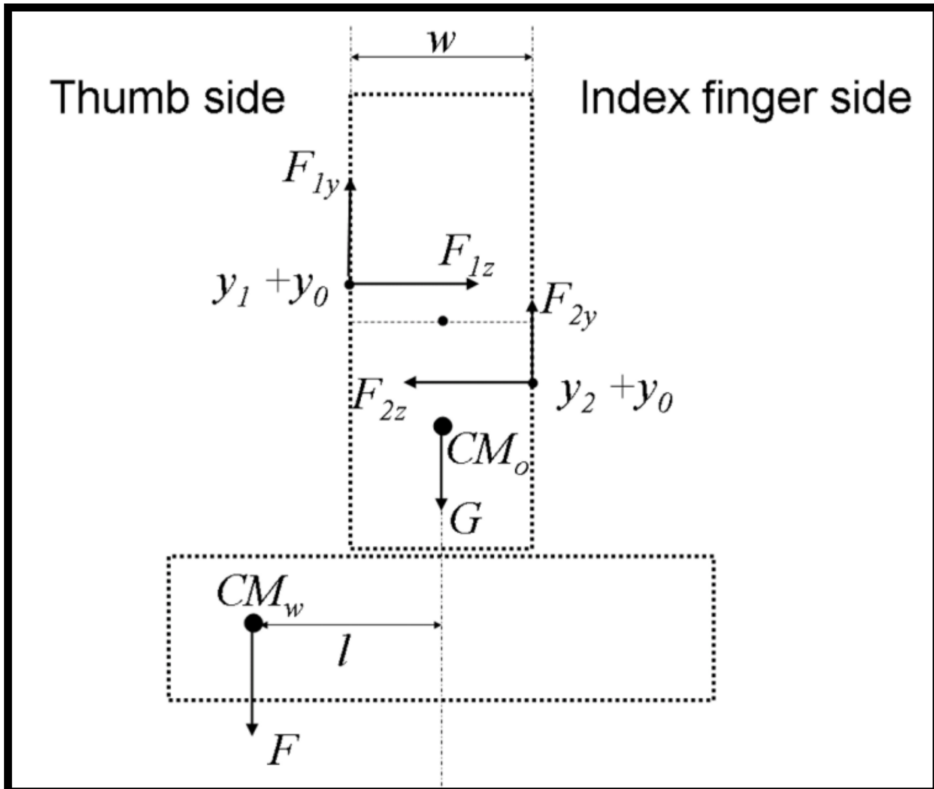
$$F_{1z} \approx F_{2z} \approx F_{GF} = (F_{1z} + F_{2z})/2 \quad (2)$$

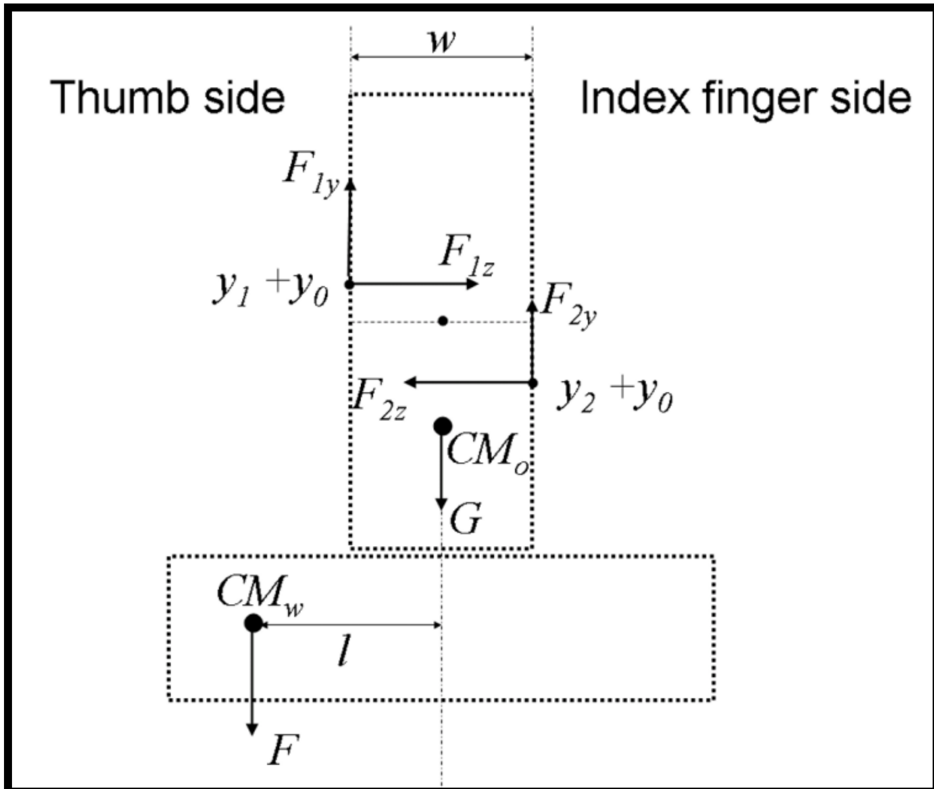


Perfect anticipation at object lift onset: $M_{com} = -M_{ext}$

$$M_{com} = \frac{w}{2}F_{1y} - \frac{w}{2}F_{2y} + (y_1 + y_0)F_{1z} - (y_2 + y_0)F_{2z} \quad (1)$$

$$F_{1z} \approx F_{2z} \approx F_{GF} = (F_{1z} + F_{2z})/2 \quad (2)$$

$$M_{com} = \frac{w}{2}d_{LF} + d_y F_{GF} \quad (3)$$



Perfect anticipation at object lift onset: $M_{com} = -M_{ext}$

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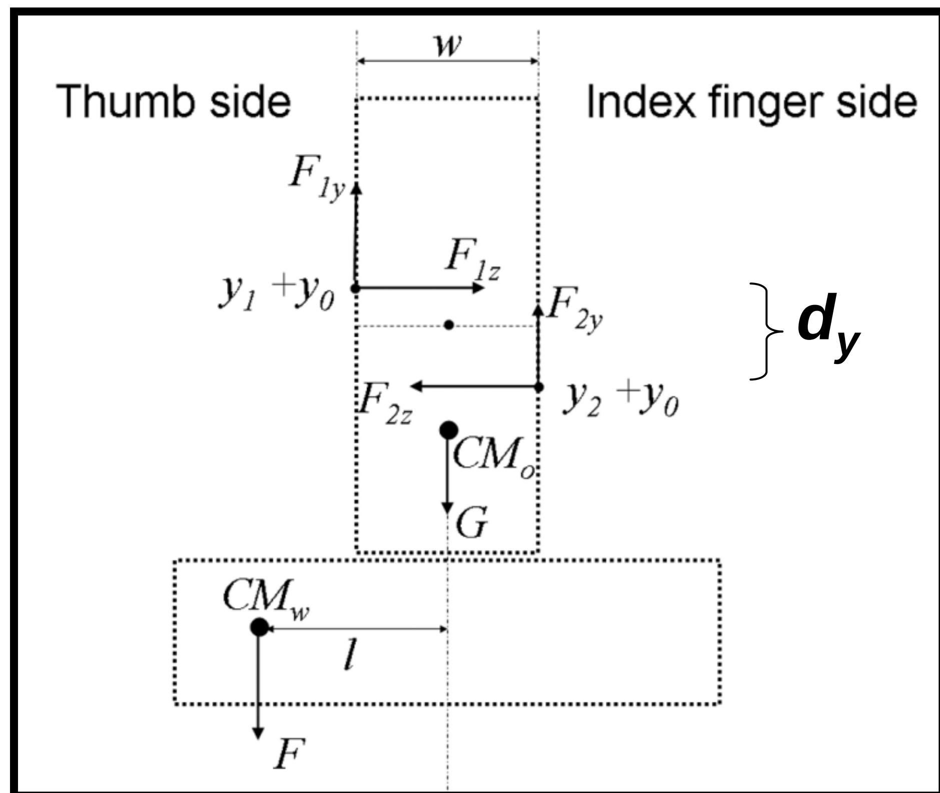
$$F_{1z} \approx F_{2z} \approx F_{GF} = (F_{1z} + F_{2z})/2 \qquad (2)$$

$$M_{com} = \underbrace{\frac{w}{2}d_{LF}}_{\boldsymbol{M_{LF}}} + \underbrace{d_y F_{GF}}_{\boldsymbol{M_{GF}}} \qquad (3)$$

moment generated by **load forces**

moment generated by **normal forces**



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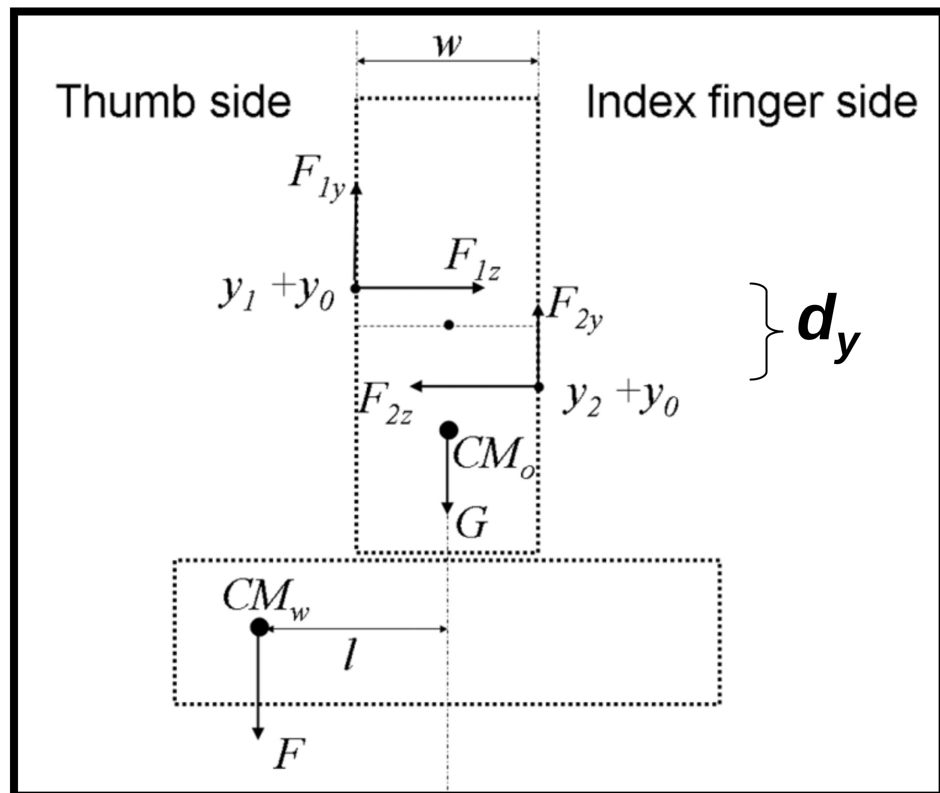
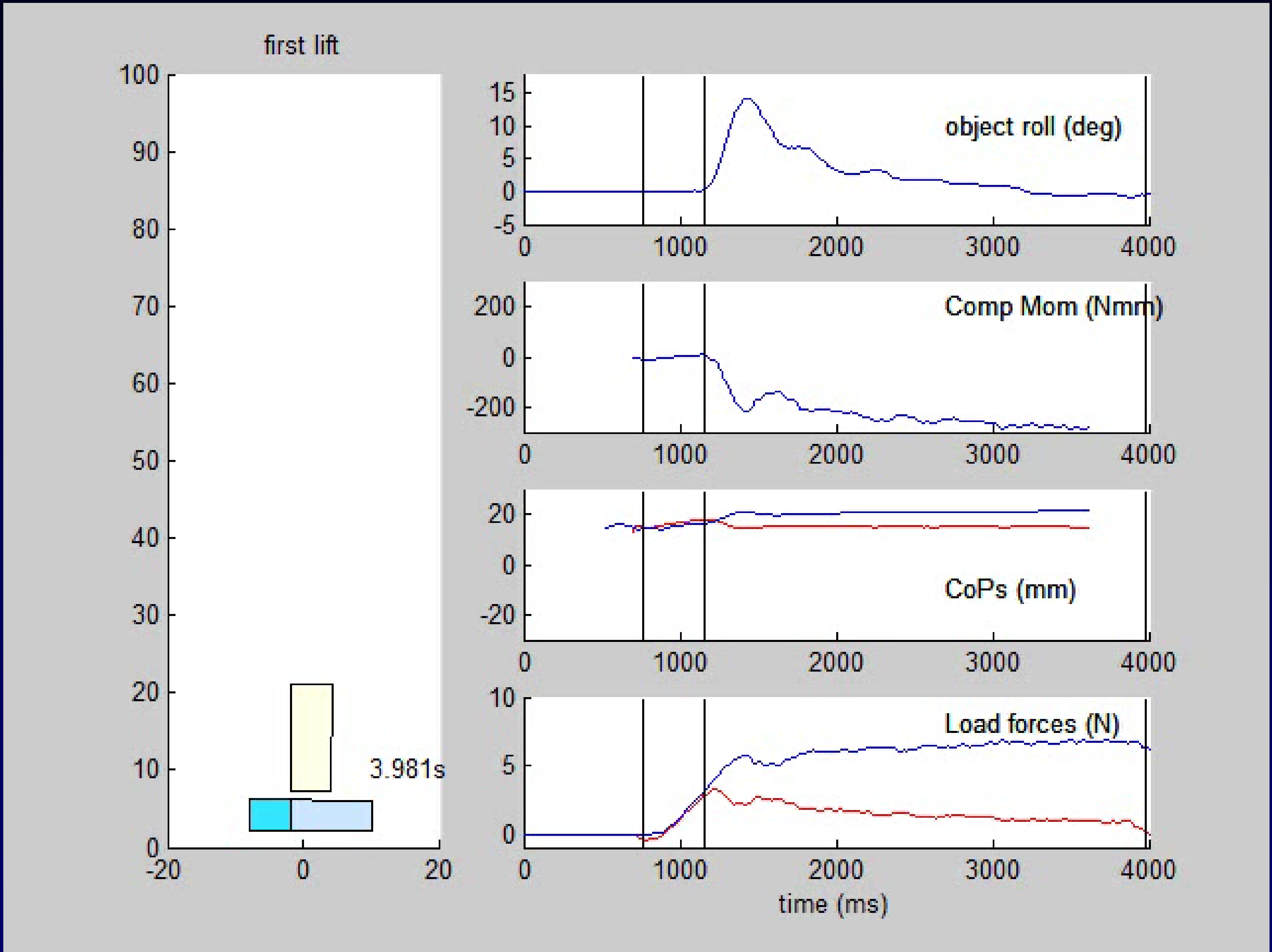
function of **load force sharing** ($F_{1y} - F_{2y}$)

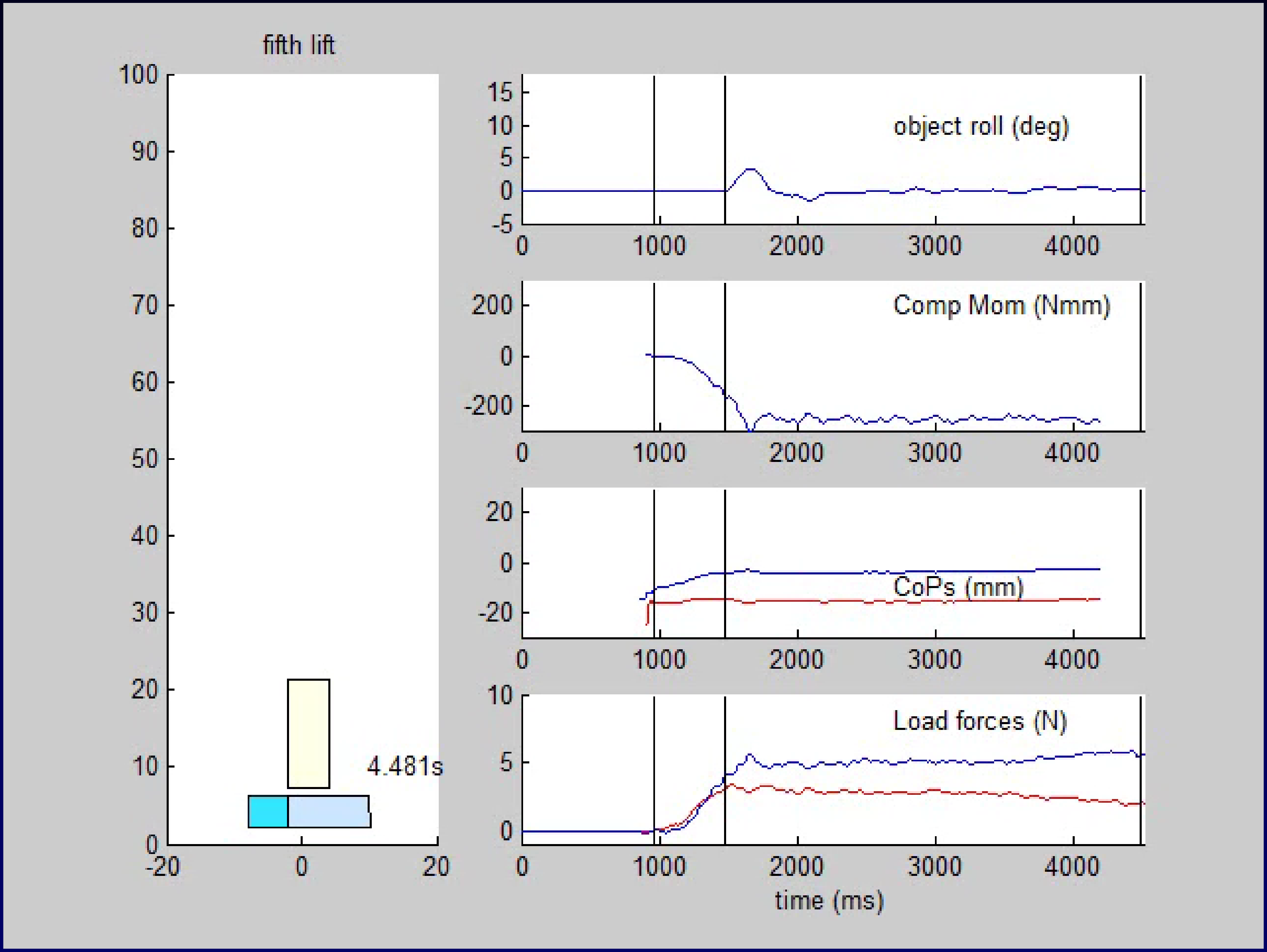
function of **normal force** *and* **vertical distance between digit centers of pressure** (d_y)



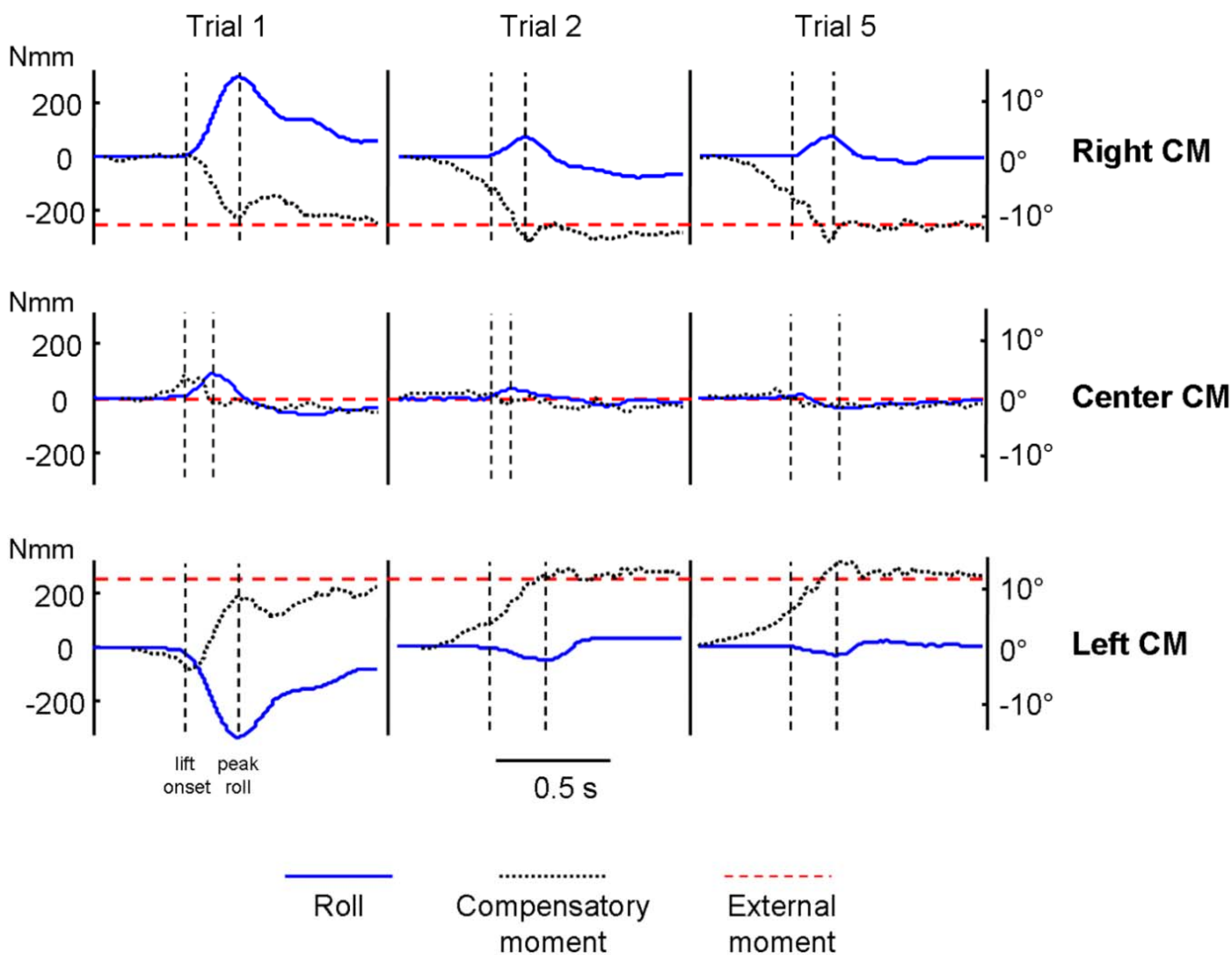
Coordination of digit placement and forces
Trial 1



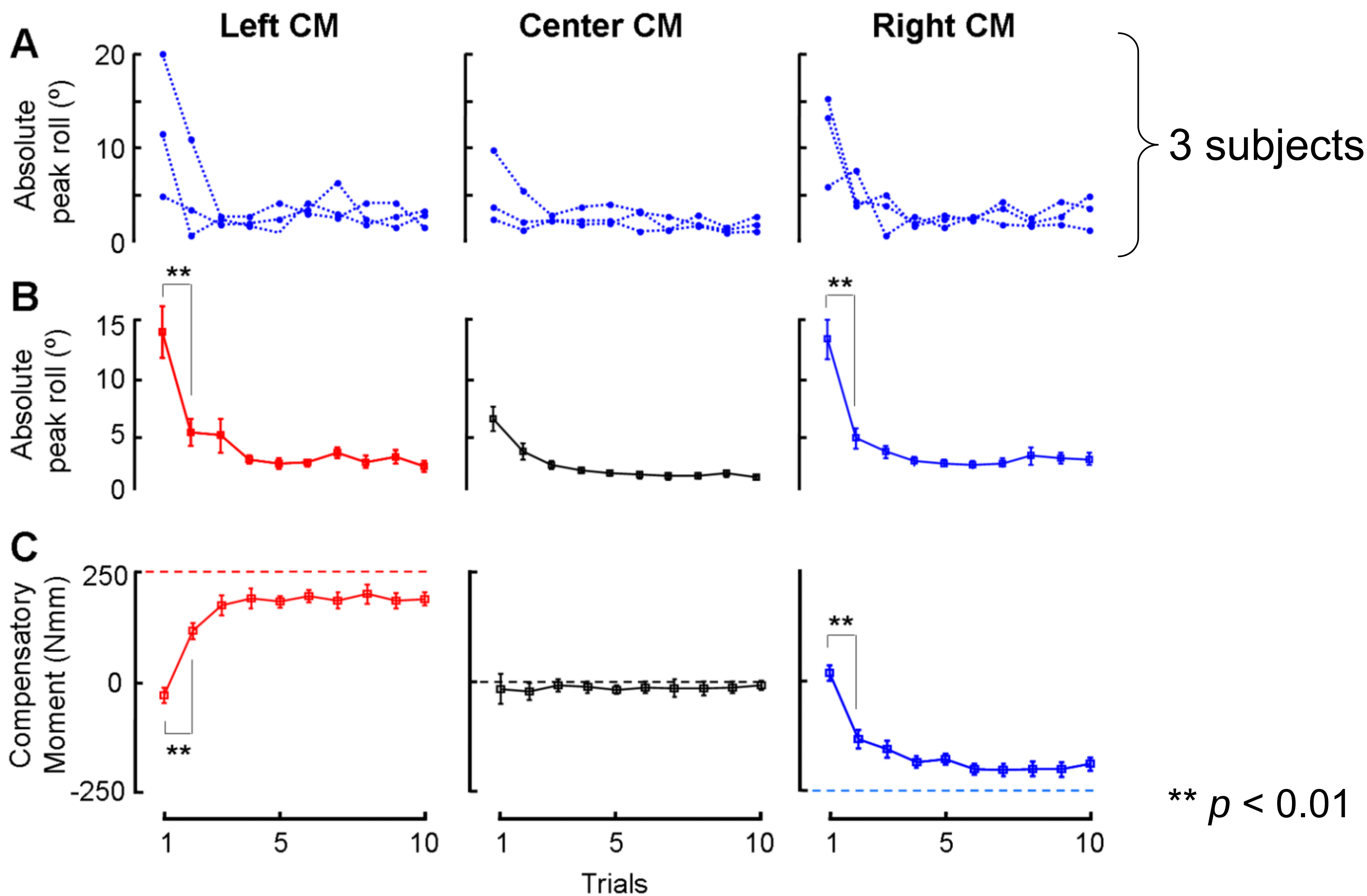
Coordination of digit placement and forces
Trial 5



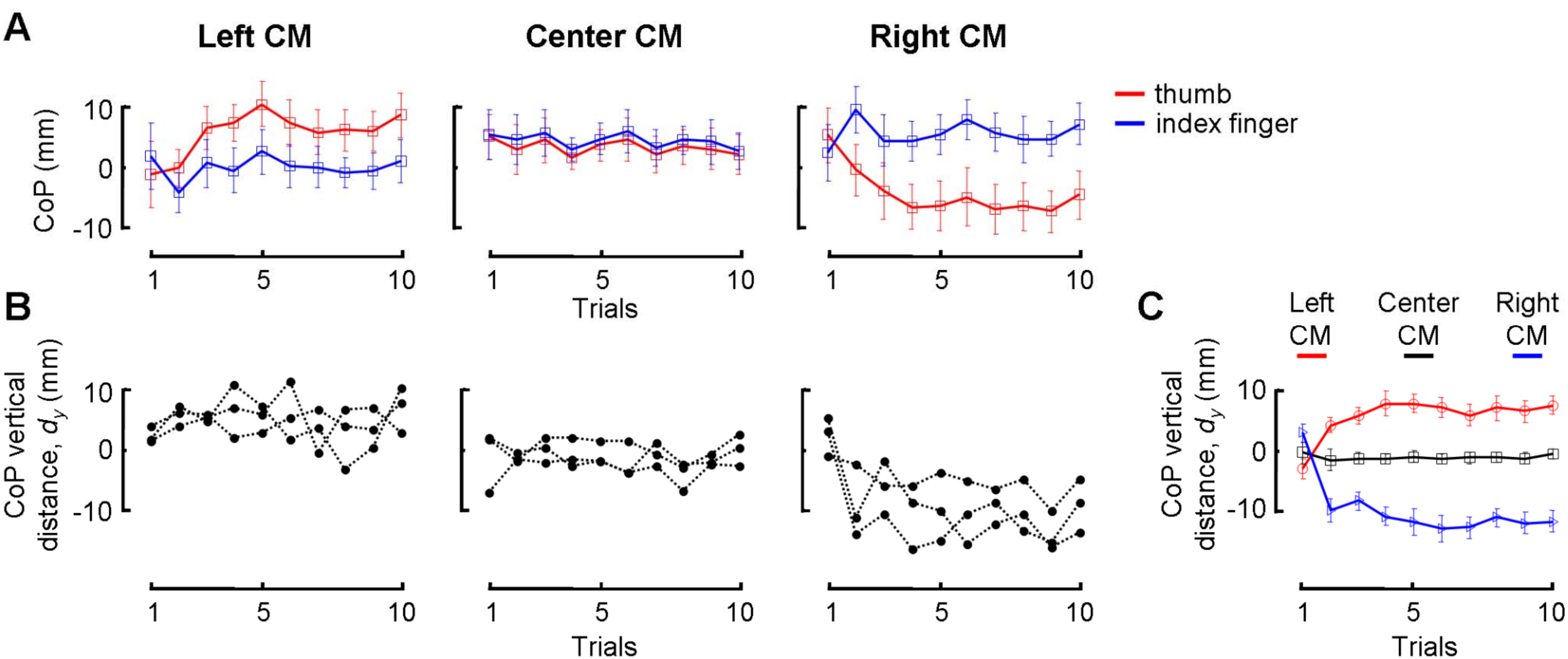
Compensatory moment and grasp performance as a function of trial (1 subject)



Subjects learn to minimize object roll within the first 3 lifts

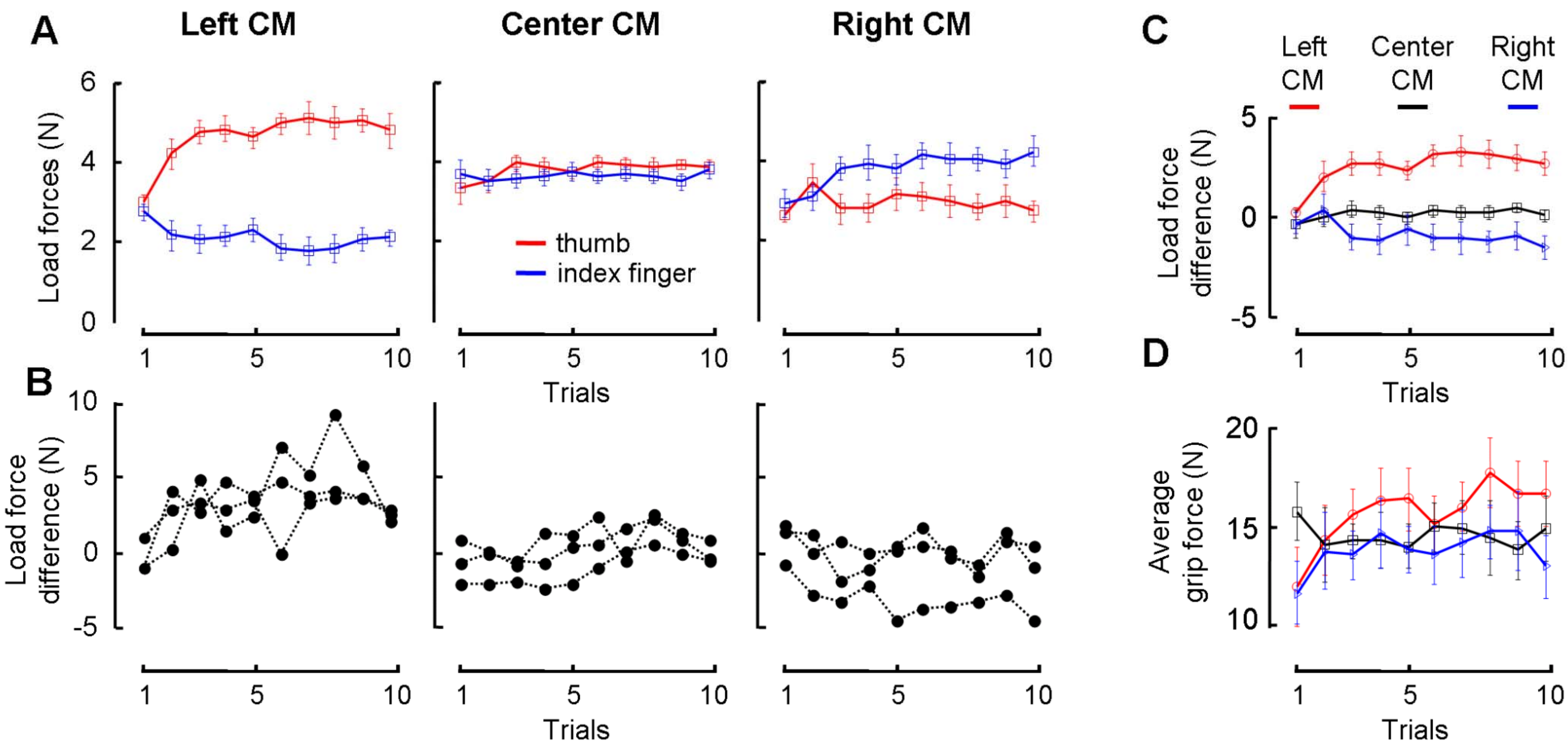


Subjects change the distance between the digit centers of pressure as a function of *trial* and *object CM location*



CM × Trial interaction on $\boldsymbol{d_y}$, $p < 0.01$
Trial 1 ≠ Trial 2 through 10, right and left CM

Subjects change the digit load force distribution as a function of *trial* and *object CM location*

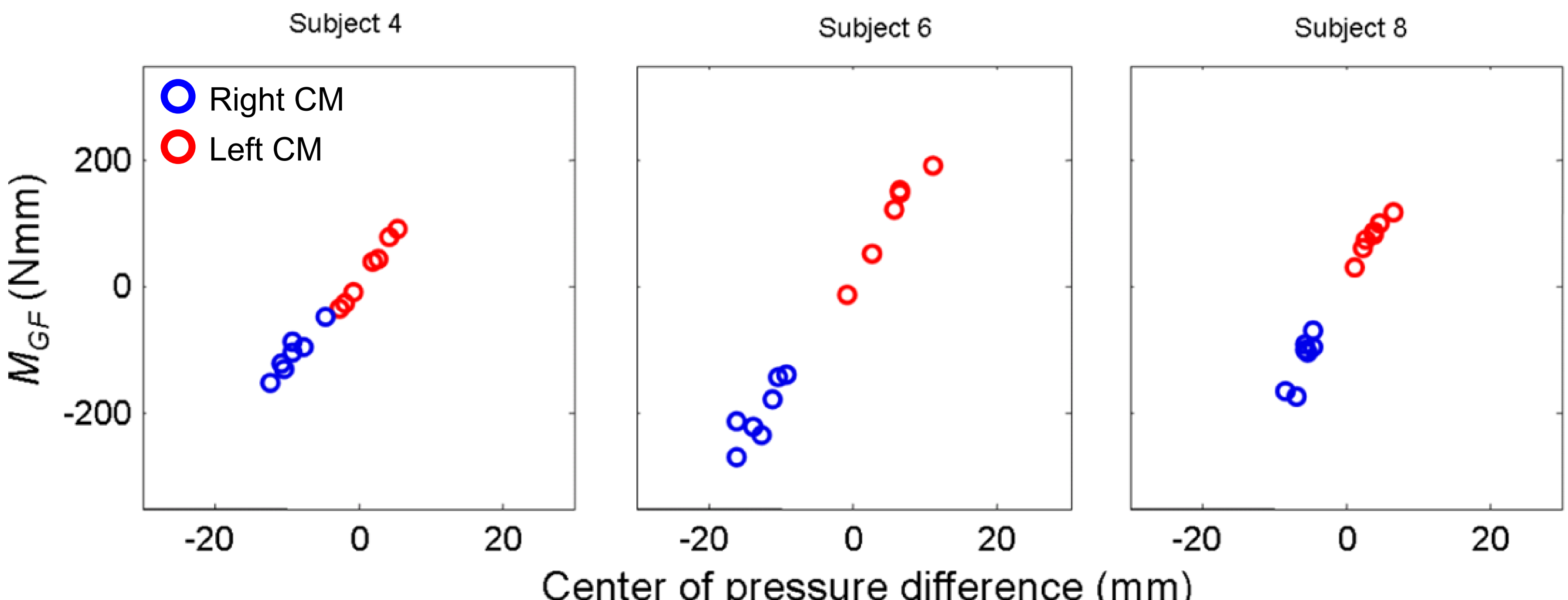


CM × Trial interaction on $\boldsymbol{d_{LF}}$, $p < 0.01$

Trial 1 ≠ Trial 2 through 10, right and left CM

The modulation of the vertical distance between the digits' CoP played a major role in the moment generated by grip forces

The trial-to-trial variability of M_{GF} was associated with trial-to-trial variability in the relative position of the digits.

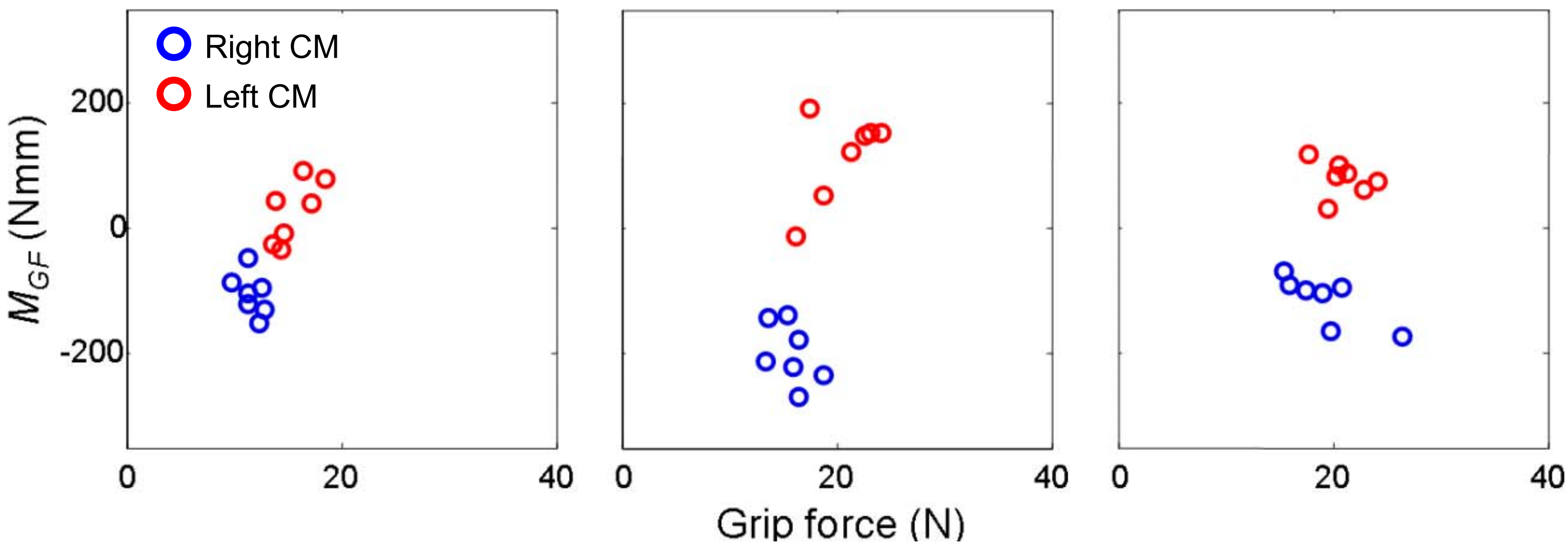


Trials 4 through 10

r-value > 0.8, $p < 0.05$ (88% of regressions)

Trial-to-trial fluctuations in the moment generated by grip forces was not due to systematic modulation of grip forces

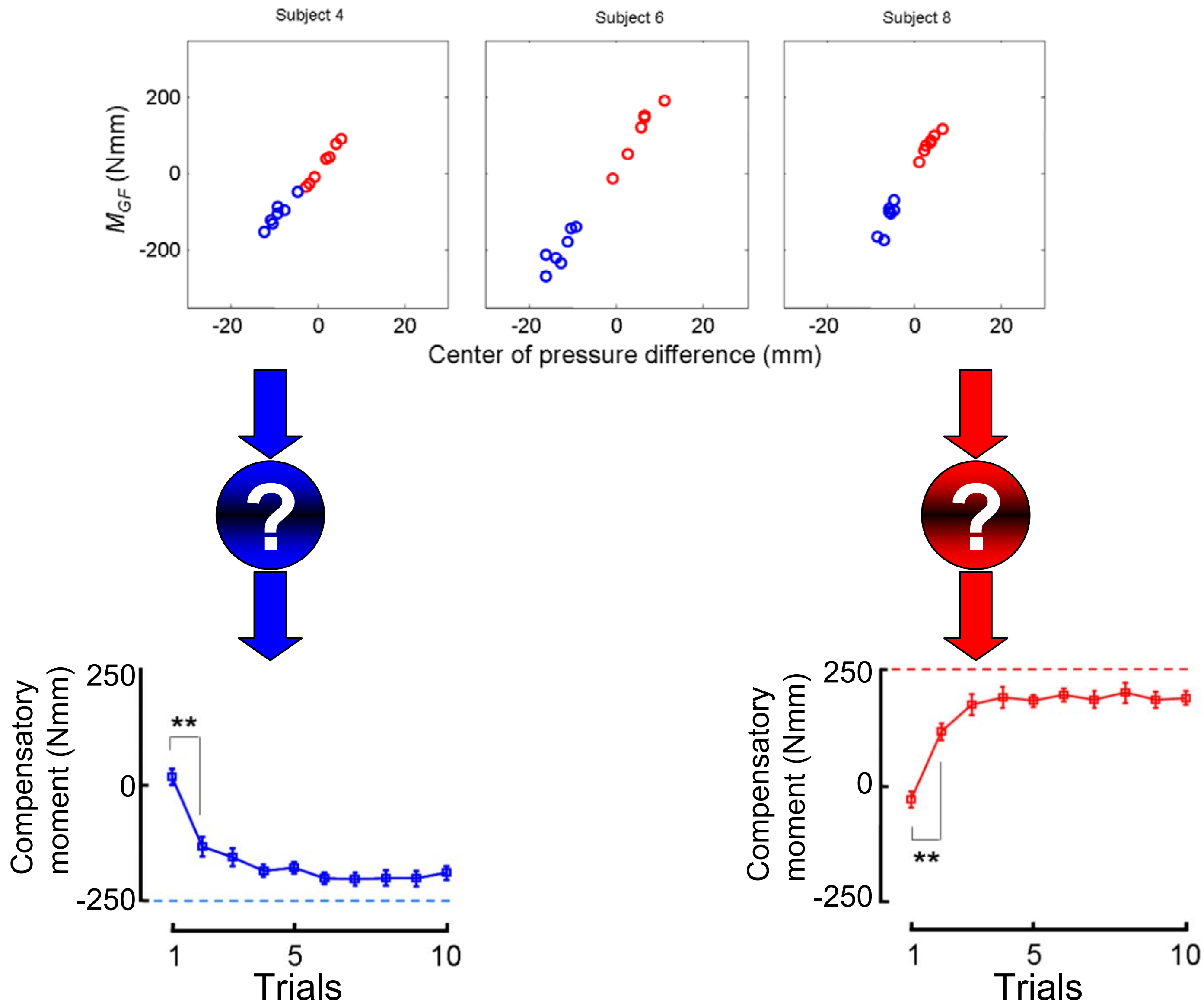
This data suggests that variability in digit positions affected the trial-to-trial repeatability of M_{GF} more than variability in grip forces.



Trials 4 through 10

r-value ± 0.6, p > 0.05 (79% of regressions)

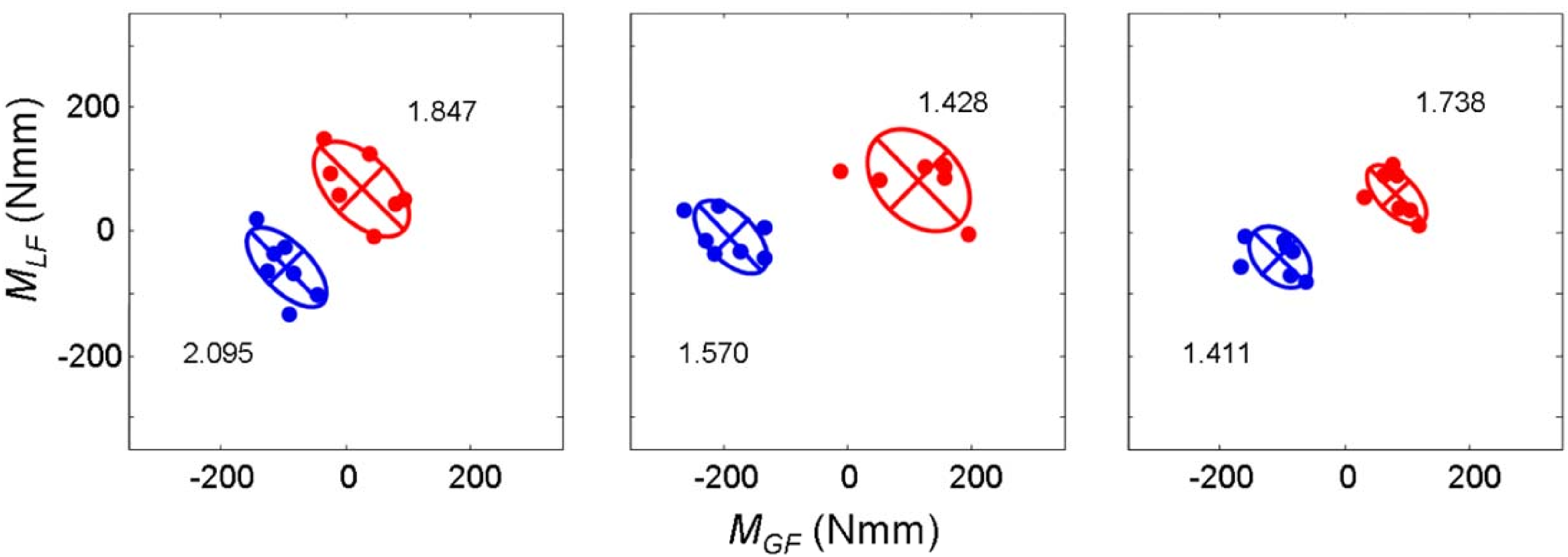
Subjects were able to generate similar compensatory moments *despite* relatively large across-trial variability in both CoP and load forces. How was this attained?



We found a negative covariation between M_{GF} (i.e., primarily dy) and M_{LF} (dLF), such that

$$\mu = \sigma(M_{LF} - M_{GF}) > \sigma(MLF + MGF) \qquad (p < 0.001)$$

Therefore, the trial-to-trial variability of the compensatory moment was significantly smaller than the trial-to-trial variability of either moment component. **This implies that digit forces modulation was dependent not only on sensorimotor memories of prior trial(s) but also on actual digit position.**



The sensorimotor processes revealed by the present study might account for our fundamental ability to manipulate objects despite variable digit positions in everyday grasping and tool use.

We propose that **learning** and **performance** of skilled object manipulation both require *integration of digit position sensing* with *sensorimorimotor memories* to select forces necessary to generate a given object dynamics.

Conclusions, Study #1

Our data suggest that subjects learned anticipatory grasp control by integrating sensorimotor memories from previous trials with feedback-driven corrections.

A theoretical framework that accounts for our results is as follows:

• digit positions and forces are learned in parallel, hence generating **a memory representation of both variables combined**

• the initial digit placement is driven primarily by **online vision** and **sensorimotor memories** from previous trials

• after contact, a comparison is made between **expected (desired) vs. actual feedback of digit placement**

• a mismatch would trigger **a change in the planned digit forces** and possibly **update sensorimotor memories.**

We propose that the sensorimotor processes revealed by the present study might account for our fundamental ability to manipulate objects despite variable digit positions in everyday grasping and tool use.

Further work is needed to test the extent to which our model can be generalized to a wider variety of manipulations.

Summary: Human Grasping

- Anticipatory control mechanisms of hand kinematics ***and*** kinetics play a fundamental role in the control of object manipulation.

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- However, online sensory feedback of digit force and position appears to be required to compensate for trial-to-trial variability in digit placement.

- Anticipatory control mechanisms play a fundamental role in the control of object manipulation.

- However, online sensory feedback appears to be required at critical time points to compensate for trial-to-trial variability in digit placement.

- Reliance on online sensory feedback is necessary even when prior information about object properties is fully available.

- Anticipatory control mechanisms play a fundamental role in the control of object manipulation.

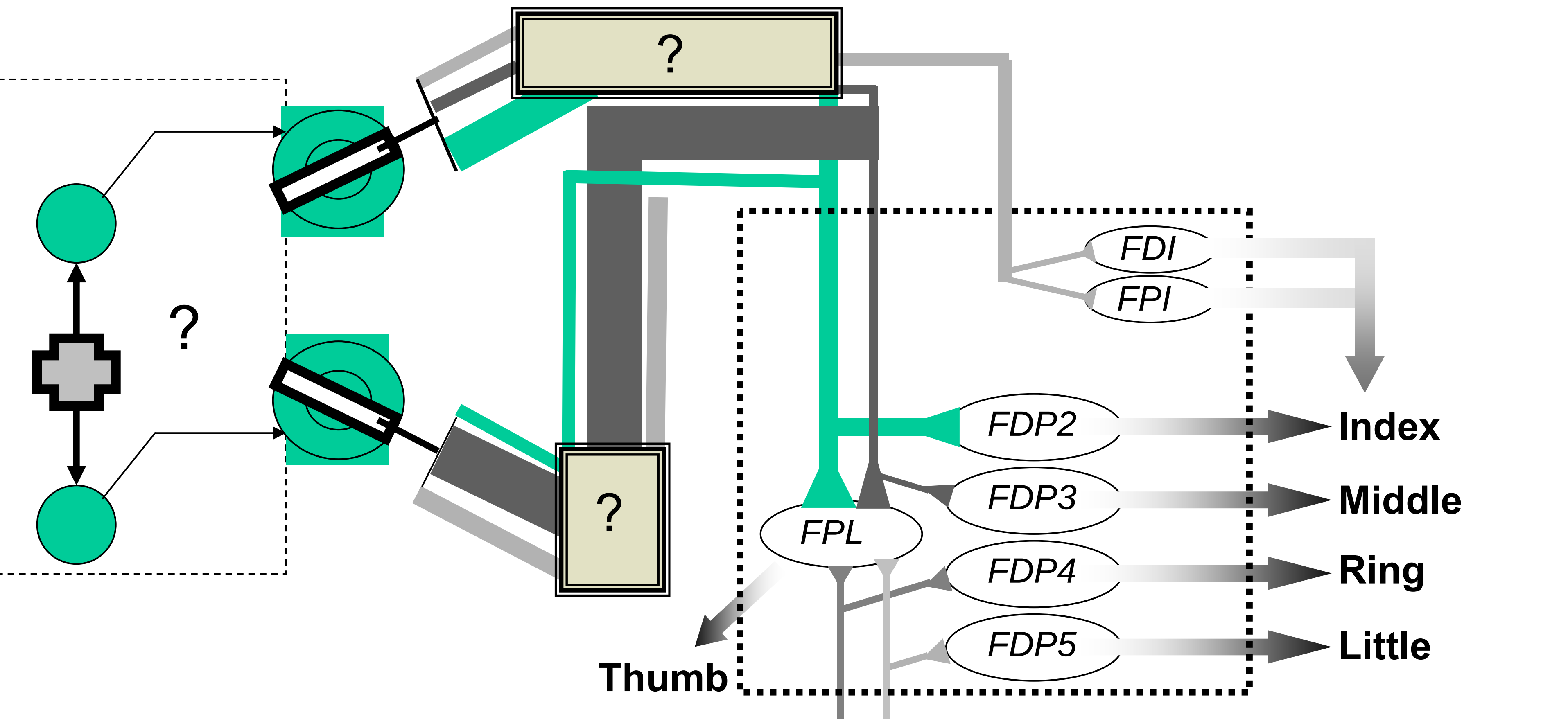
- However, online sensory feedback appears to be required at critical time points to compensate for trial-to-trial variability in digit placement.

- Reliance on online sensory feedback is necessary even when prior information about object properties is fully available.

- Tasks requiring the retrieval of learned digit position suggests an independent sensory memory representations from digit forces.

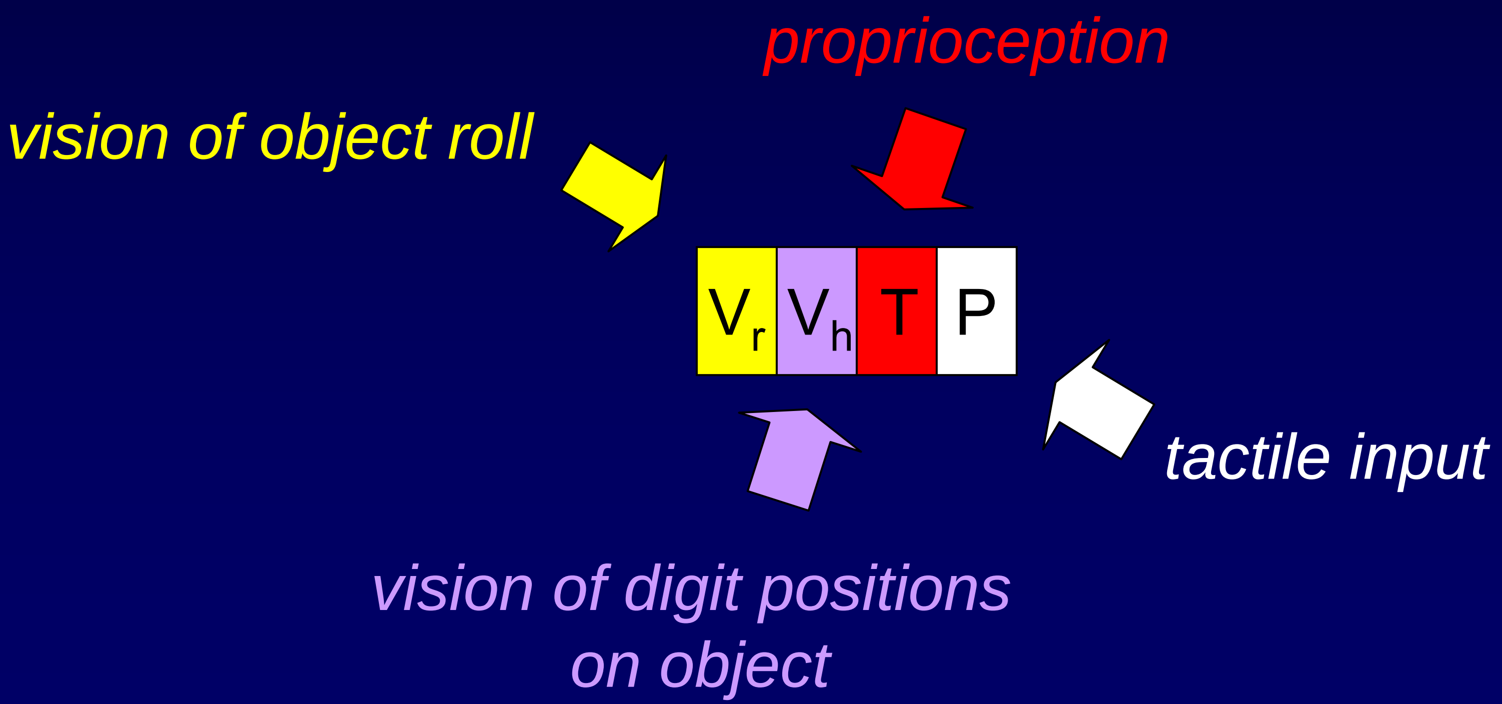
Open questions (1)

- What are the main cortical networks associated with the distribution and/or modulation of common neural input to simultaneously active hand muscles?



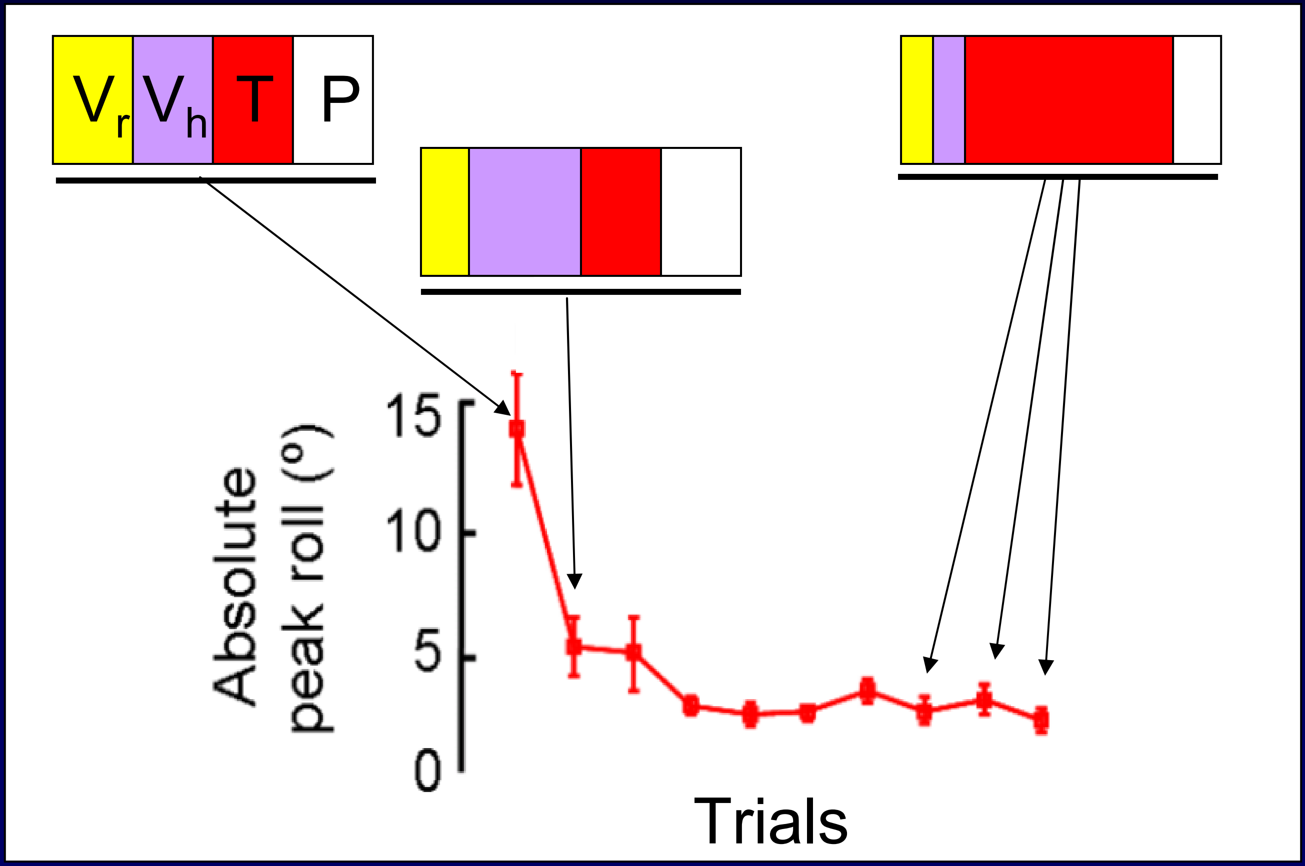
Open questions (2)

• What is the relative weight of sensory modalities involved in learning the relationship between digit positions and forces?



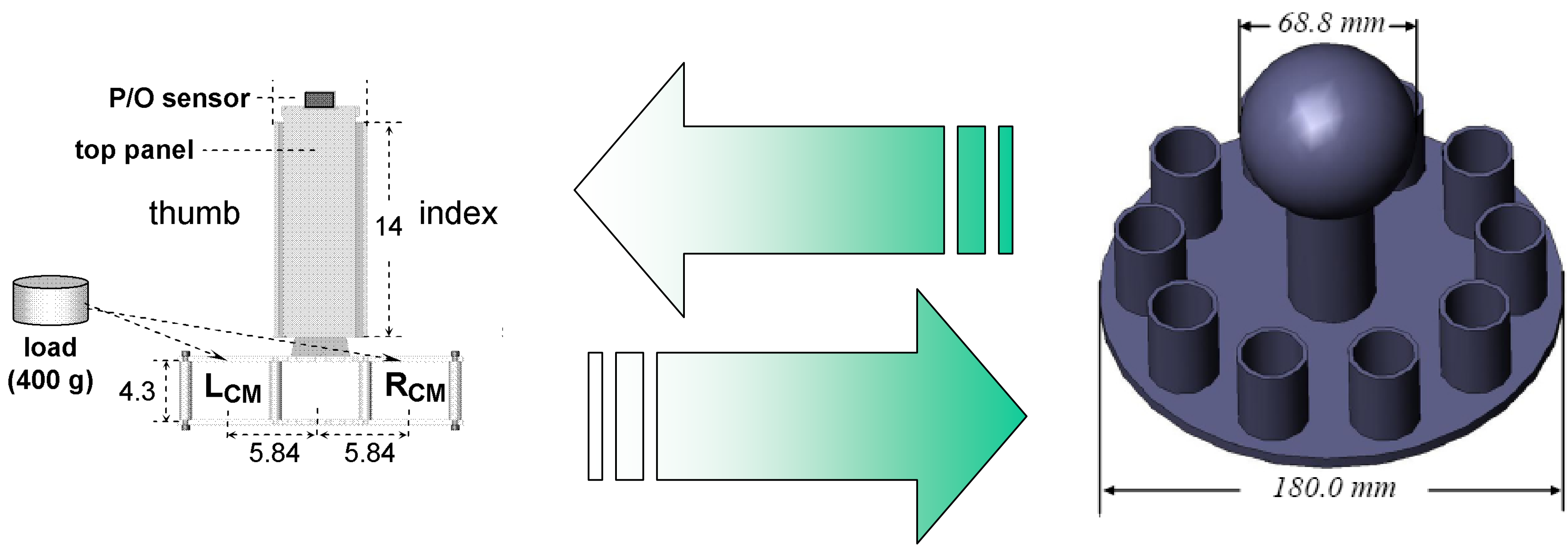
Open questions (3)

• How does the relative weight of each sensory modality change as a function of practice?



Open questions (4)

• How do sensorimotor memories affect learning and/or generalizing digit positions and forces to either a new tool or different uses of the same tool?



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