

Collège de France, Feb 1st 2011
Stanislas Dehaene Seminar



**Karolinska
Institutet**

The construction of an experience of our own body



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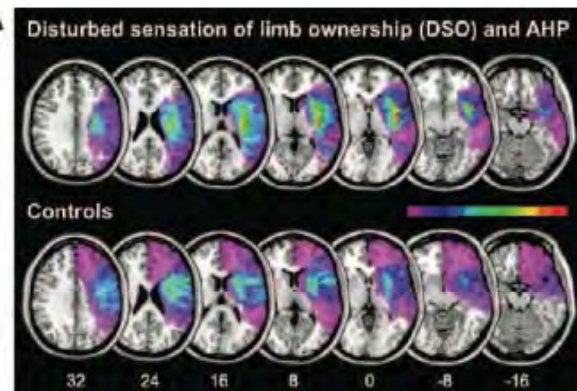
Stockholm, Sweden

Body ownership

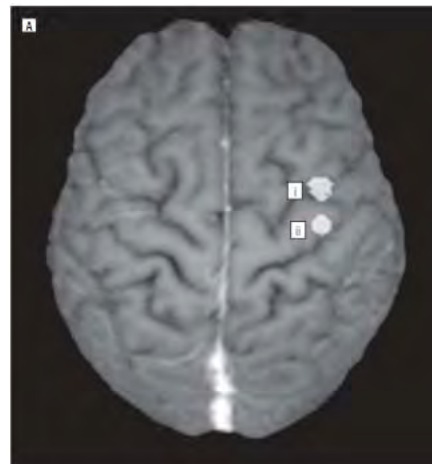


Which is my hand?

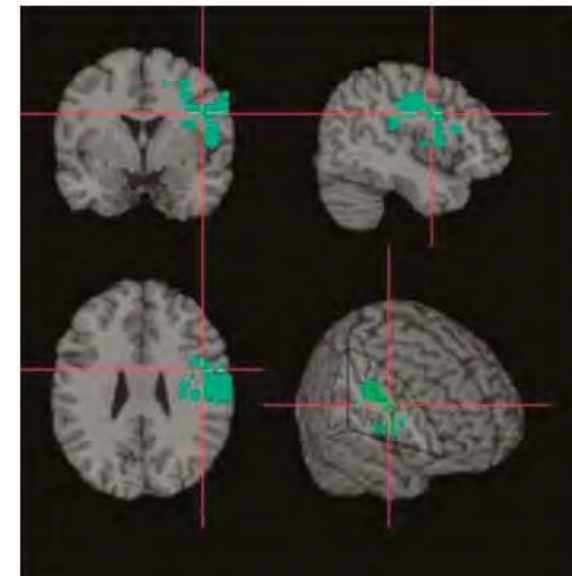
Asomatognosia and Somatoparaphrenia



Baier and Karnath (2008)
Stroke



Arzy et al, . (2006)
Arch Neurol



Berti et al. (2005) *Science*

Body ownership as a 'multisensory' problem



Which is my hand?

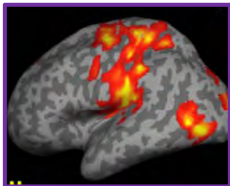
Outline



1. Body ownership as a multisensory problem



2. Behavioural evidence from psychology



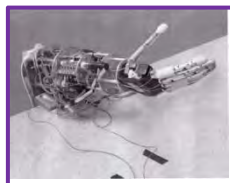
3. Multisensory responses in premotor and intraparietal areas: neurophysiology & imaging



4. Imaging illusions of limb ownership

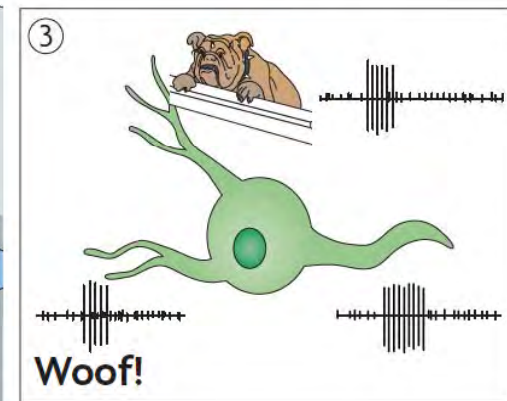
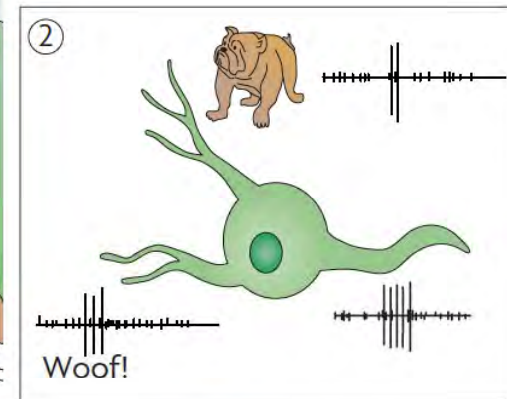
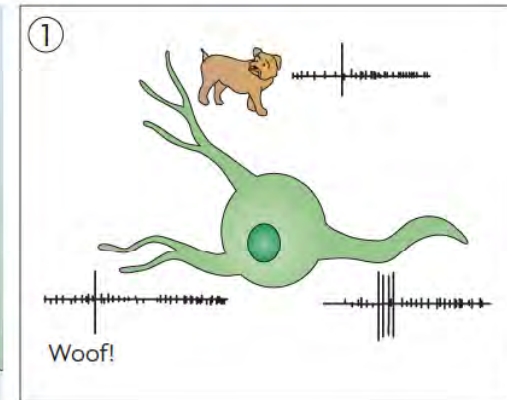
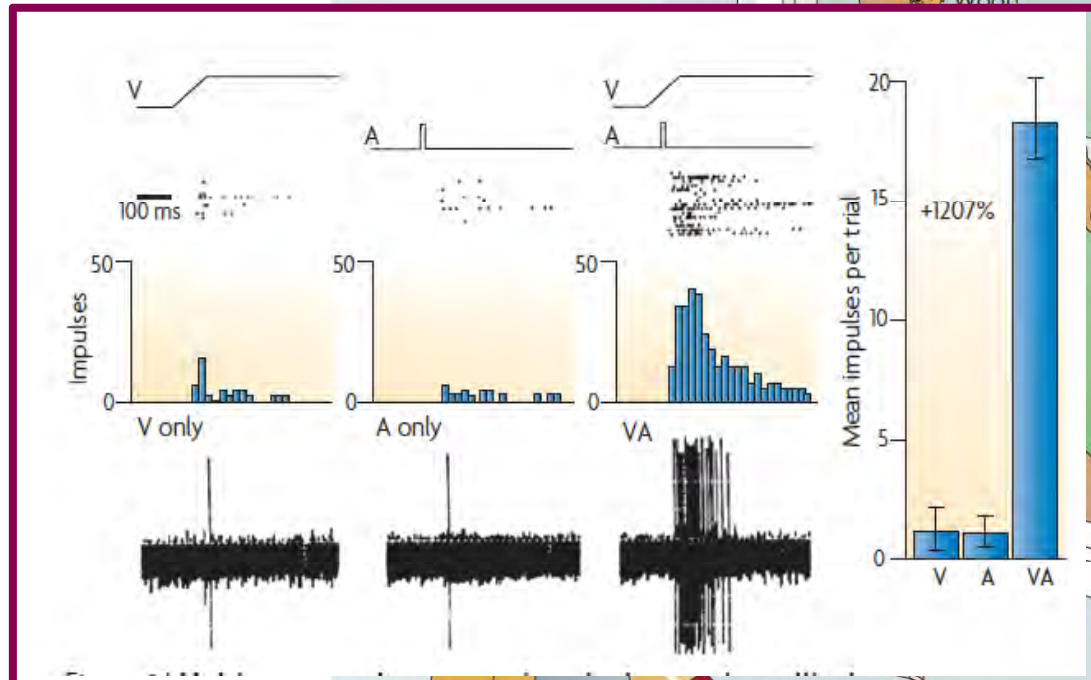


5. Behavioural & imaging studies of full-body ownership



6. Epilogue: applications to advanced prosthetics

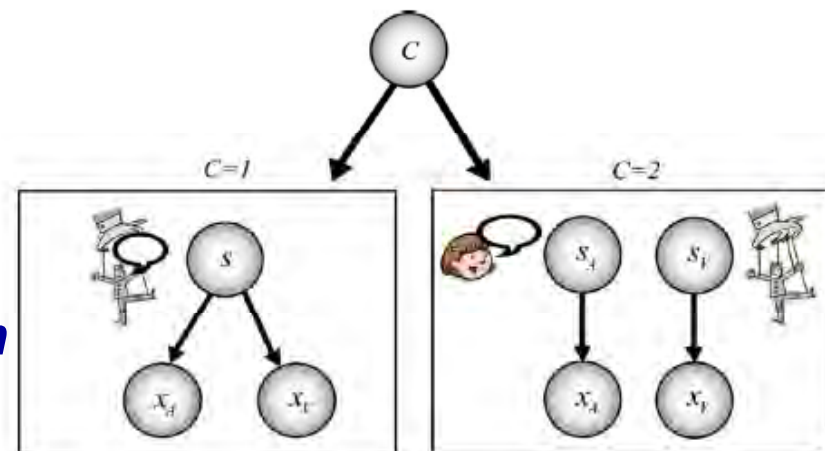
1. Key principles of multisensory integration



Stein and Stanford (2008) Nat Rev Neuroscience

Key principles of multisensory integration

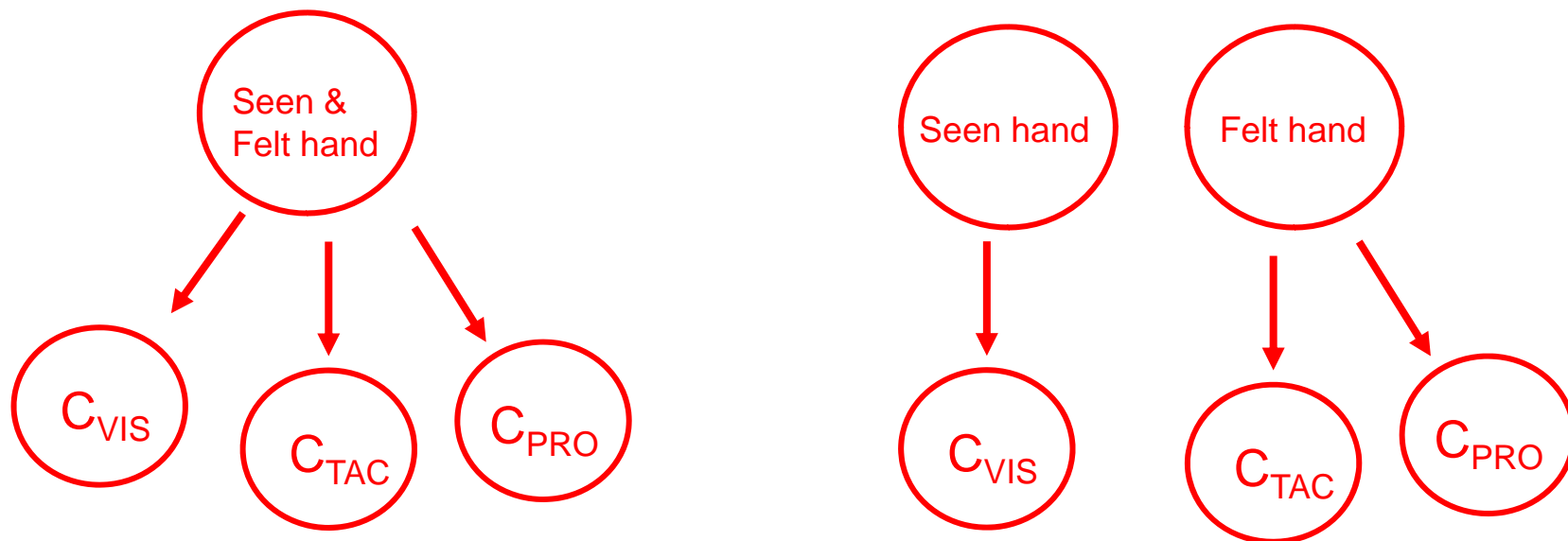
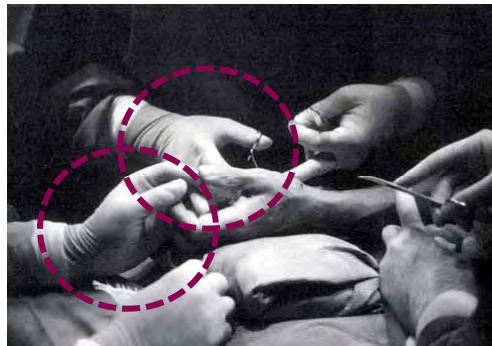
- Temporal congruency principle.
- Spatial congruency principle.
- Principle of inverse effectiveness.
- **Multisensory fusion problem.**
- **Multisensory assignment problem (causal interference problem)**



Multisensory assignment problem
From Körding et al. (2007)

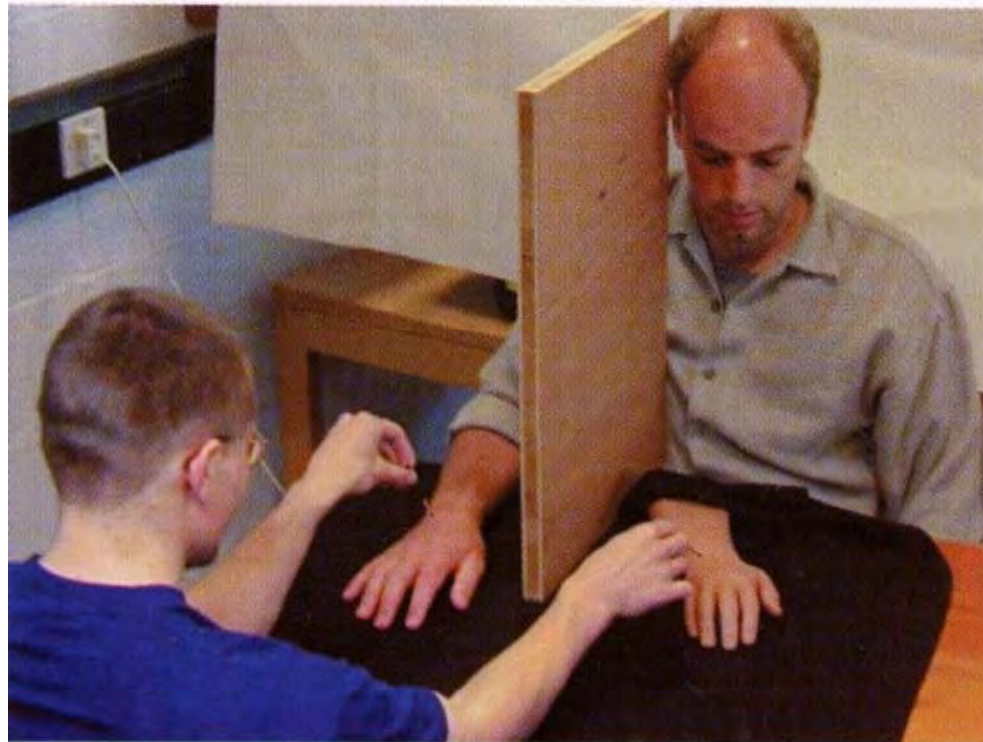
Holmes and Spence (2005)
Current Biology

Body ownership as a multisensory assignment problem



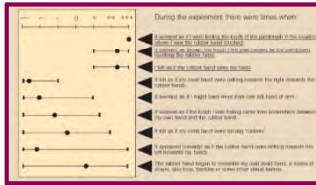
2. Behavioral evidence from experimental psychology

Rubber hand illusion

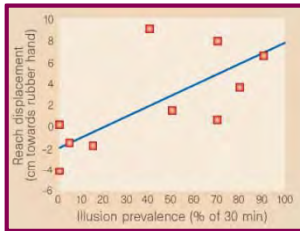


Botvinick and Cohen (1998) *Nature* 391: 756

Measures of the illusion



- Questionnaire with visual analogue scales. (Botvinick and Cohen 1998)



- Hand perceived closer to the location of the rubber hand (proprioceptive drift): pointing error when asked to point to one's hand (e.g Taskiris and Haggard 2005; Ehrsson et al. 2005)



- Emotional responses when the hand is 'threatened' or 'hurt' (e.g Armel & Ramachandran 2003; Ehrsson et al. 2009)



- Visual capture of tactile localization (cross modal congruency task) (Pavani et al 2001; Zopf et al. 2009)

Behavioural evidence that the illusion depends on integration of visual, tactile and proprioceptive information in hand-centered reference frame

Temporal congruency principle:

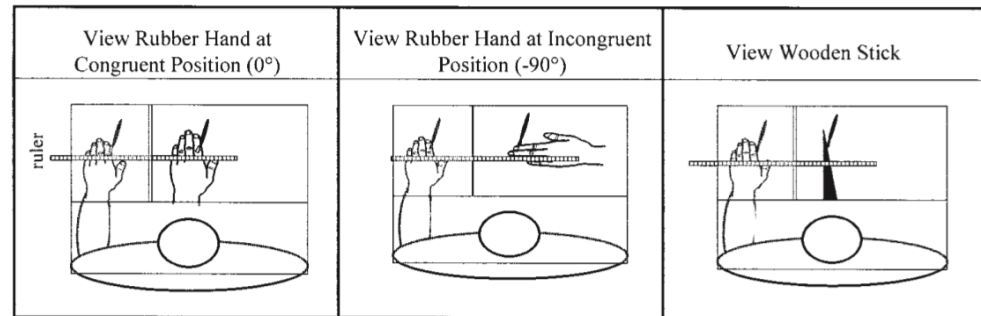
- The brushstrokes applied to the two hands must be synchronous (*temporal congruency vision-touch*)(Botvinick & Cohen 1998; Armel & Ramachandran 2003; Ehrsson et al. 2004; Tsakiris and Haggard 2005)
- Longer temporal delays break the illusion (>300 ms) (*temporal congruency vision-touch*)(Shimada et al. 2009)



Behavioural evidence that the illusion depends on integration of visual, tactile and proprioceptive information in hand-centered reference frame

Spatial congruency principle:

- The brushstrokes must be applied to corresponding parts of the two hands (*spatial congruency vision-touch*)(e.g. Ehrsson et al. 2009)
- The rubber hand must be anatomically aligned with the hidden real hand. (*spatial congruency vision-proprioception*) (Pavani et al. 2001; Ehrsson et al. 2004; Tsakiris et al. 2005)

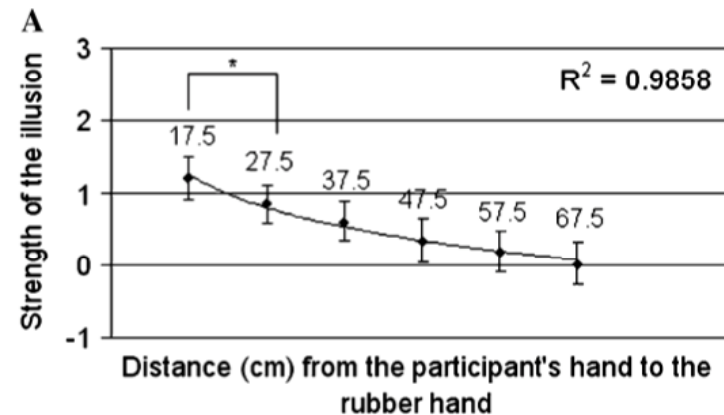
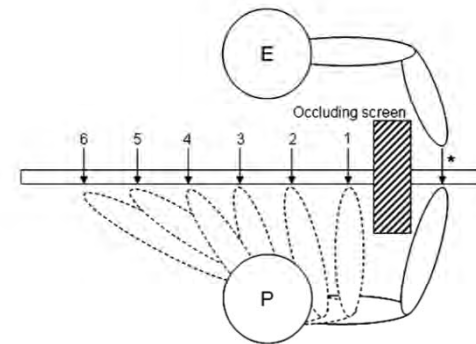


Tsakiris et al. (2005)

Behavioural evidence that the illusion depends on integration of visual, tactile and proprioceptive information in hand-centered reference frame

Hand-centered reference frames:

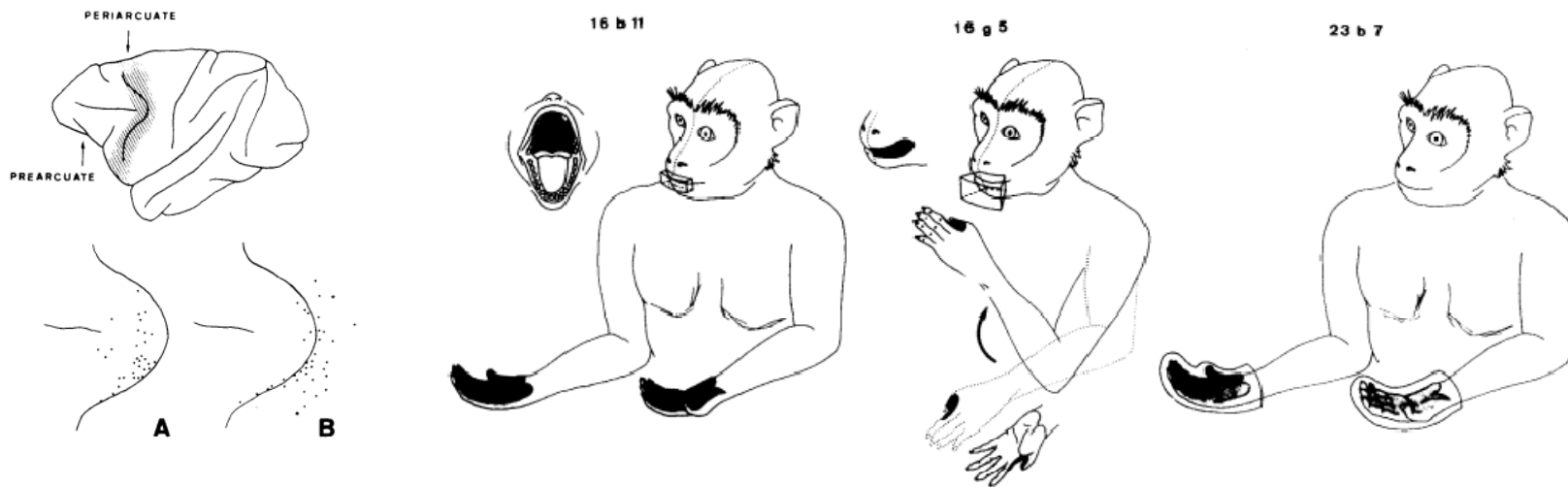
- The rubber hand is placed within reaching distance (30 cm from the real hand) (Lloyd 2007).
- The direction of the brushstrokes must congruent in hand-centered reference frames, and not in allocentric external coordinates (Constantini and Haggard 2007)



Lloyd (2008)

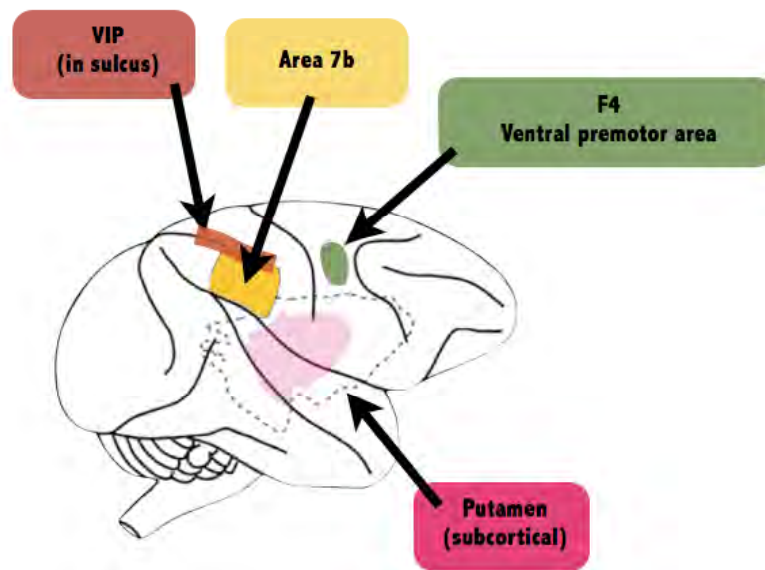
3. Neurophysiology: multisensory integration in premotor and intraparietal cortex

Multisensory neurons in premotor cortex and peri-personal space

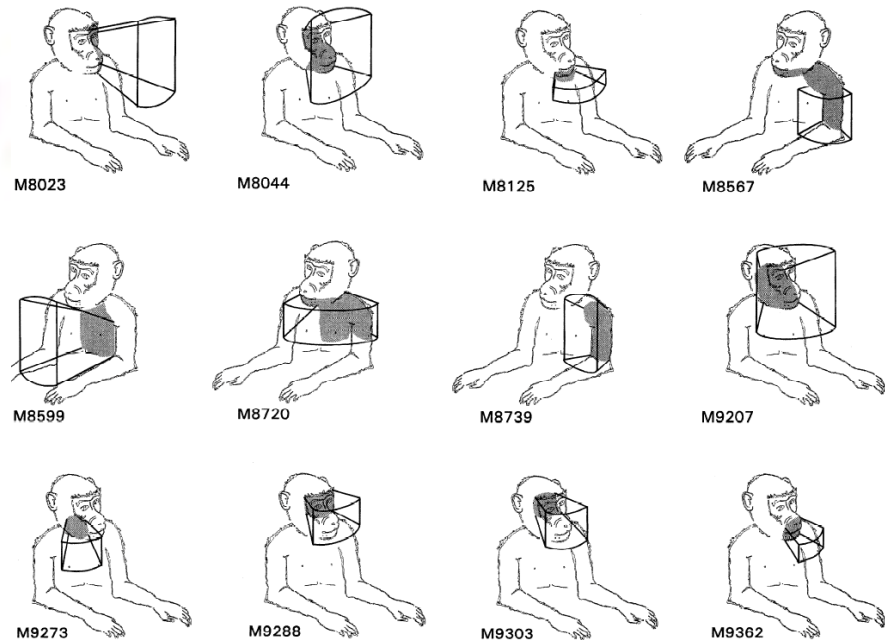


From Rizzolatti et al. (1981) Exp. Brain Res.

Multisensory neurons and peri-personal space

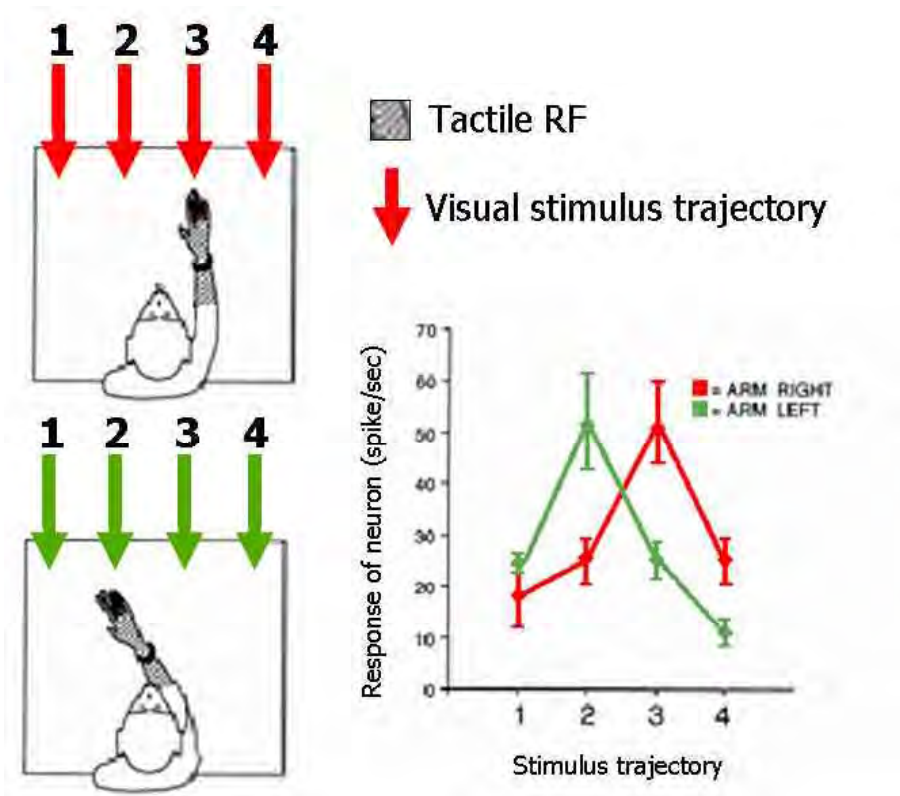
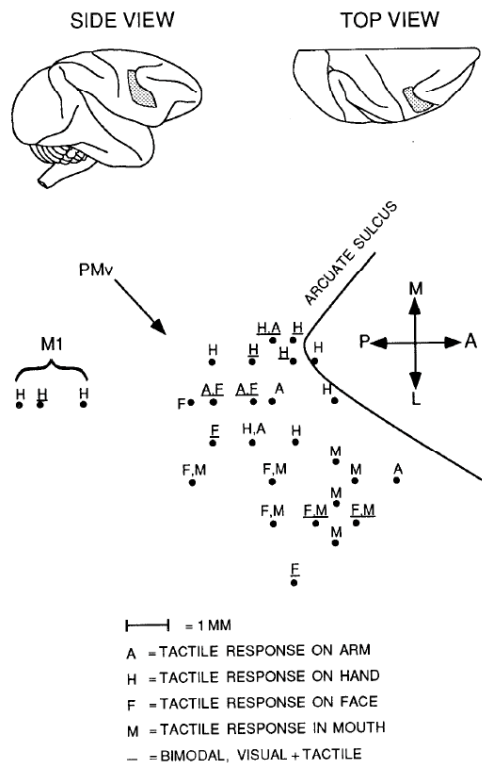


Hyvärinen & Poranen 1974
Rizzolatti et al. 1981
Graziano & Gross 1993, 1997
Duhamel et al. 1998



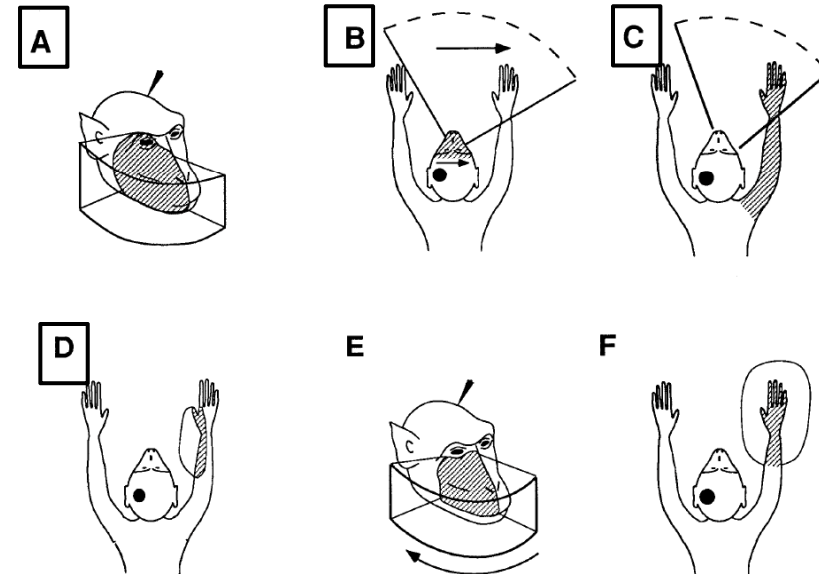
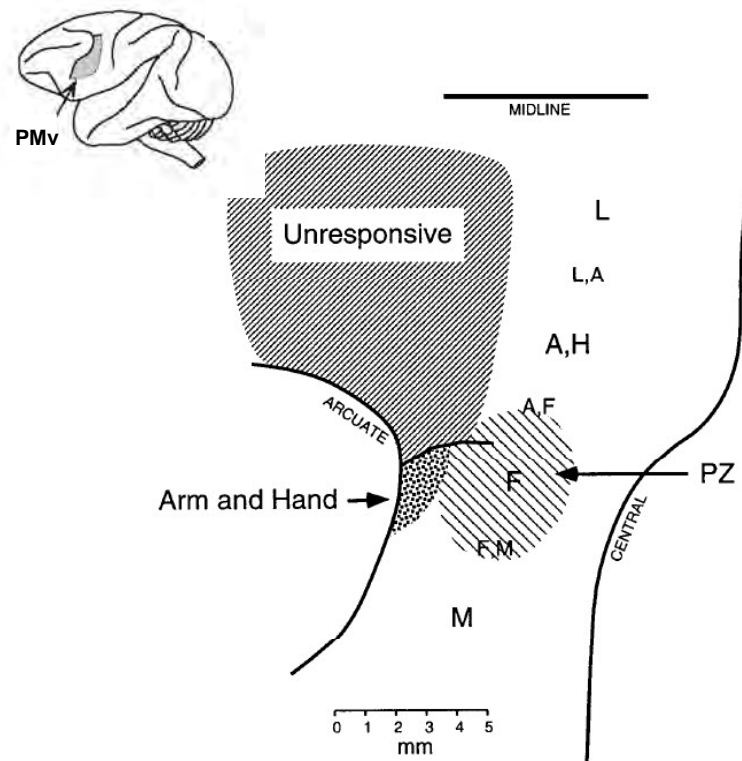
Fogassi et al. (1996) *J. Neurophysiol.*

Multisensory neurons and body-part-centered coordinates



From Graziano et al. (1997, 1999)

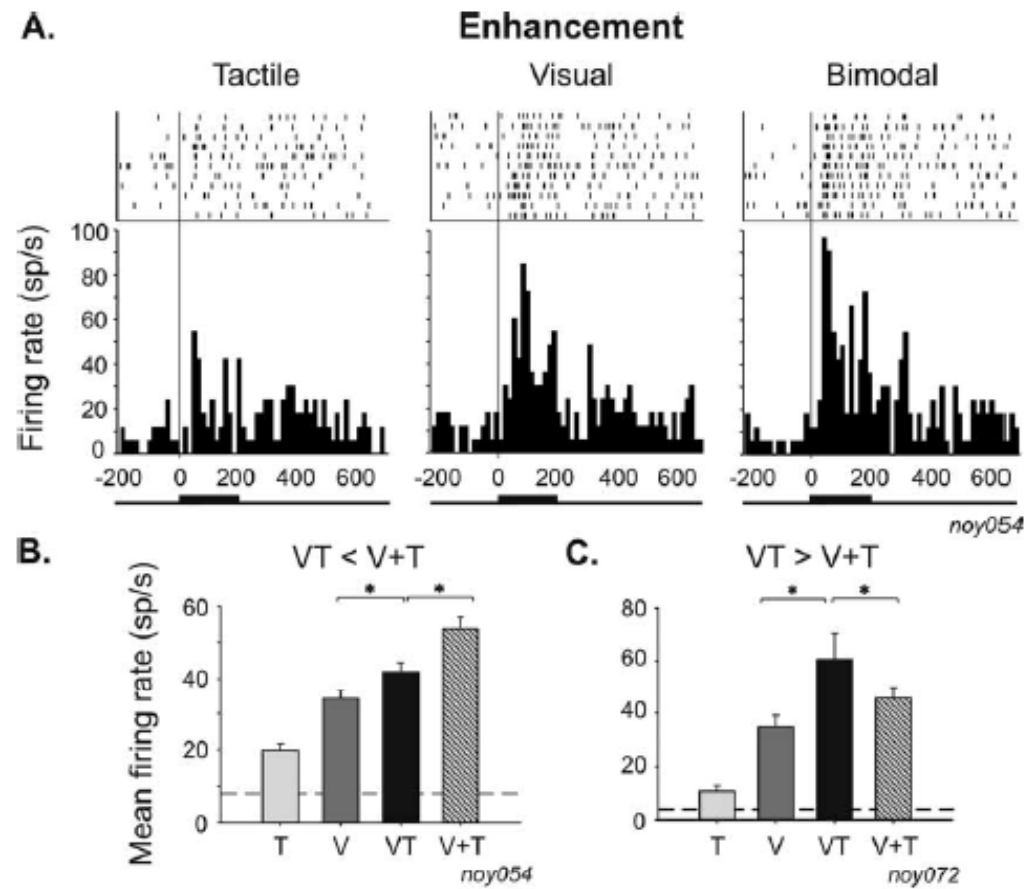
Multisensory responses in premotor cortex in anesthetized monkeys



Graziano et al. (2000) Exp. Brain Res.

Graziano et al. (2007) J. Neurophysiol.

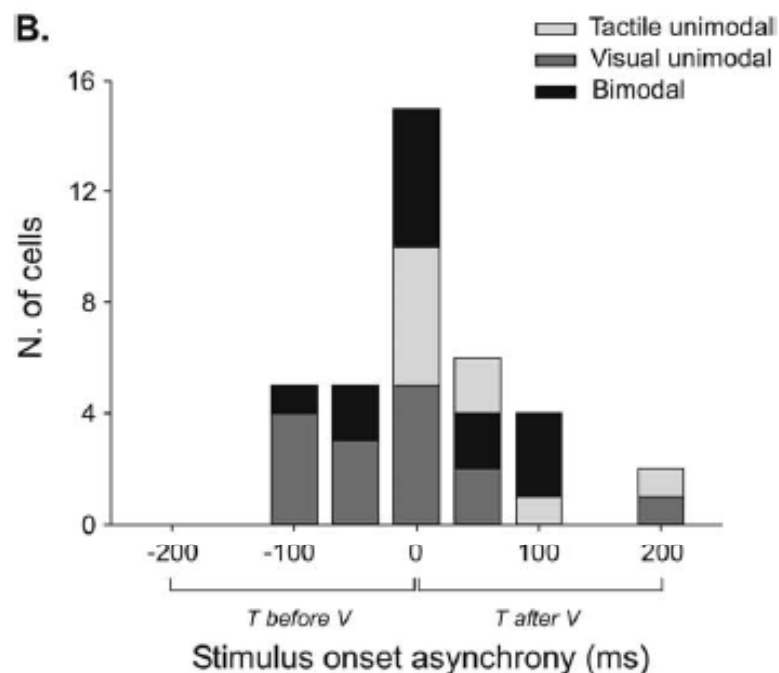
Multisensory integration in ventral intraparietal area: super-additivity



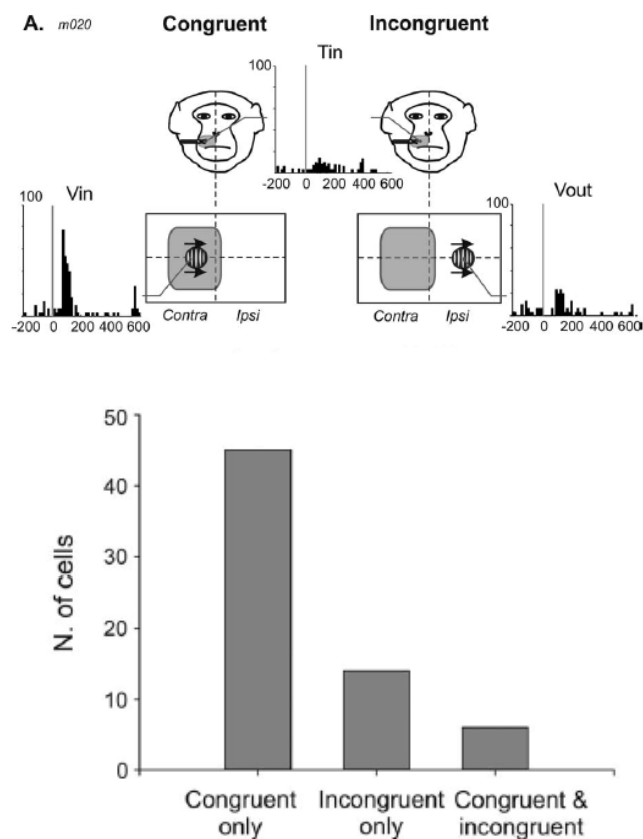
Avillac et al (2007) Nature Neuroscience

Multisensory integration in ventral intraparietal area: spatial and temporal congruency effects

Temporal congruency

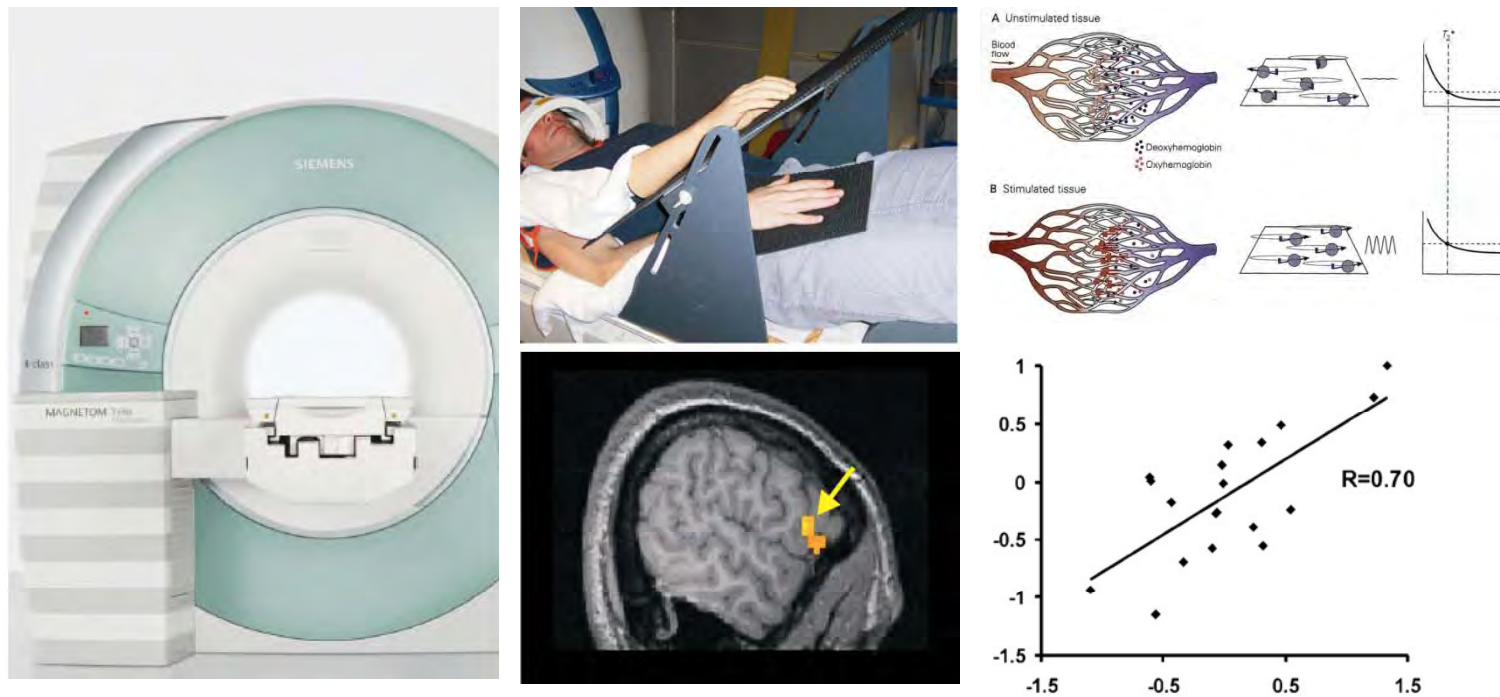


Spatial congruency



Avillac et al (2007) Nature Neuroscience

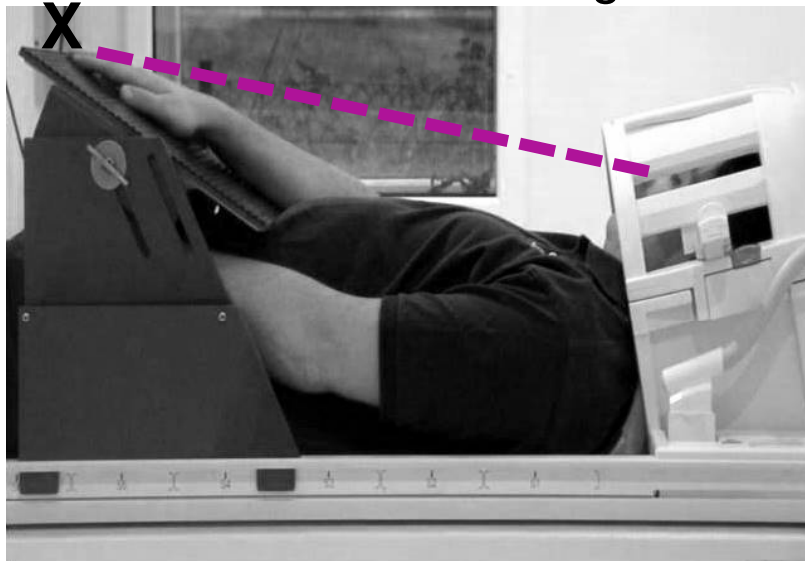
Functional magnetic resonance imaging (fMRI)



- Blood-oxygen-dependent signal (BOLD)

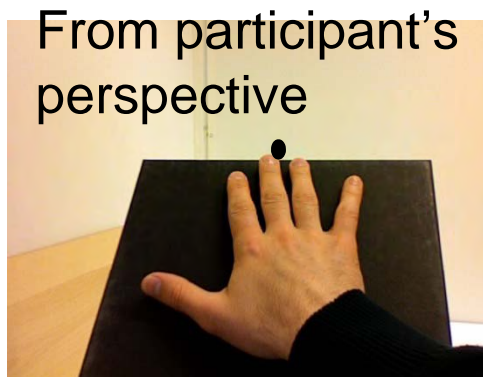
Human premotor and intraparietal cortices performs multisensory integration

Direct view of the right hand:

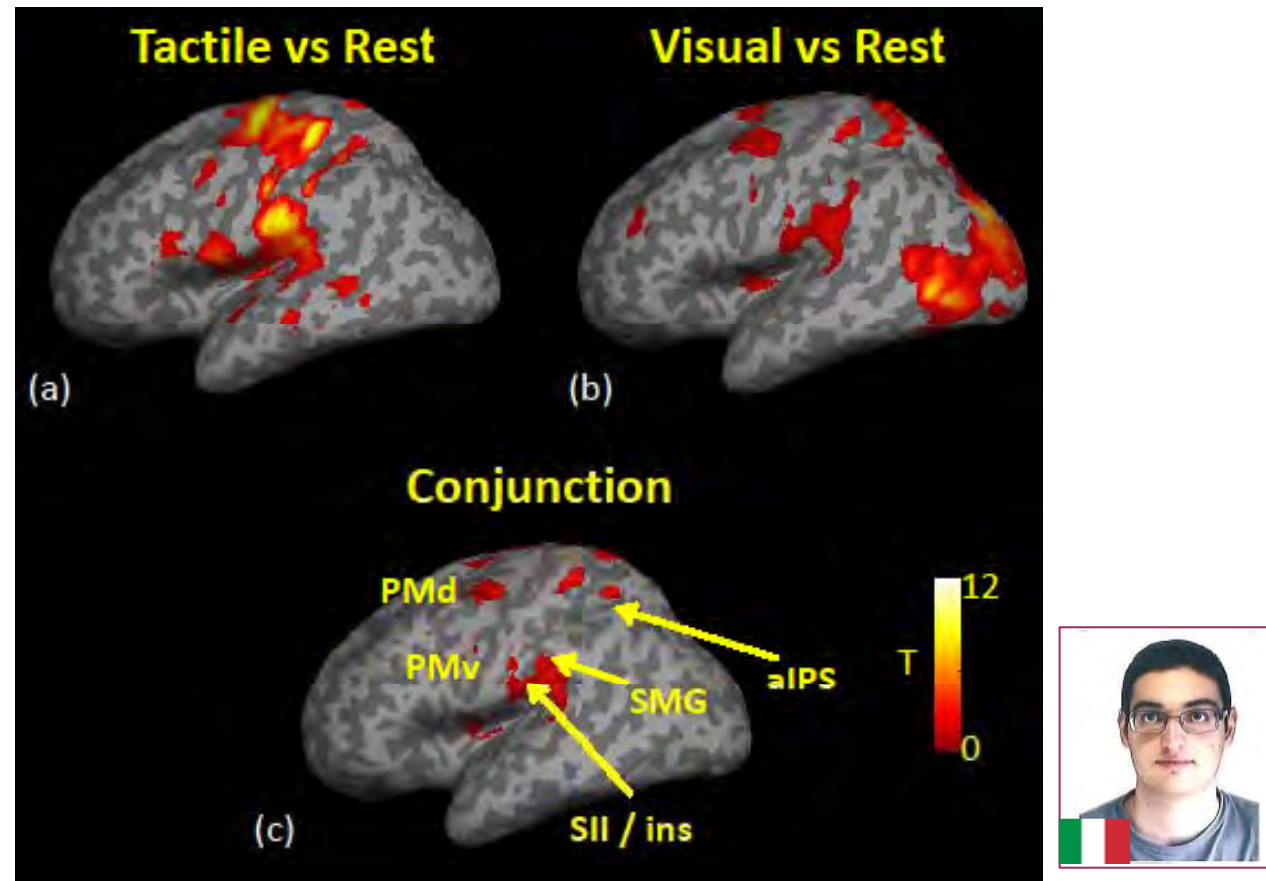


Tactile stimulation

		Absent	Present
Visual stimulation	Absent	R	T
	Present	V	VT

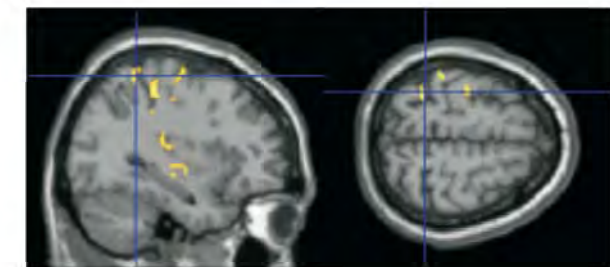
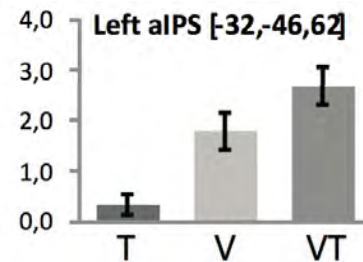
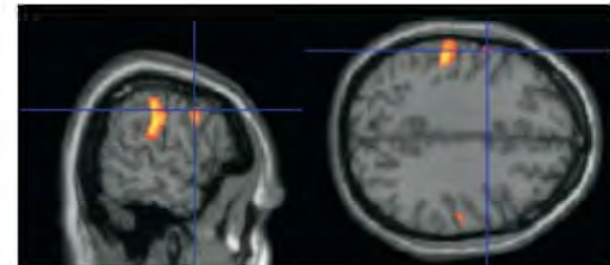
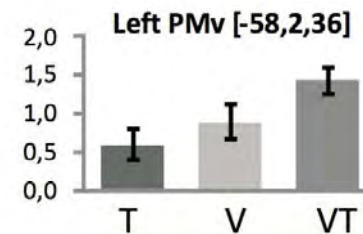
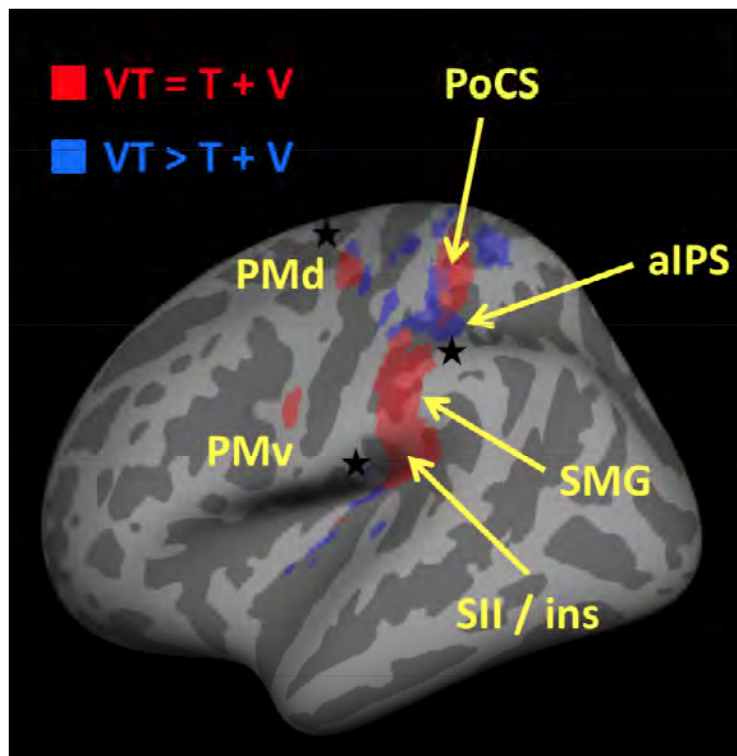


Human premotor and intraparietal cortices performs multisensory integration

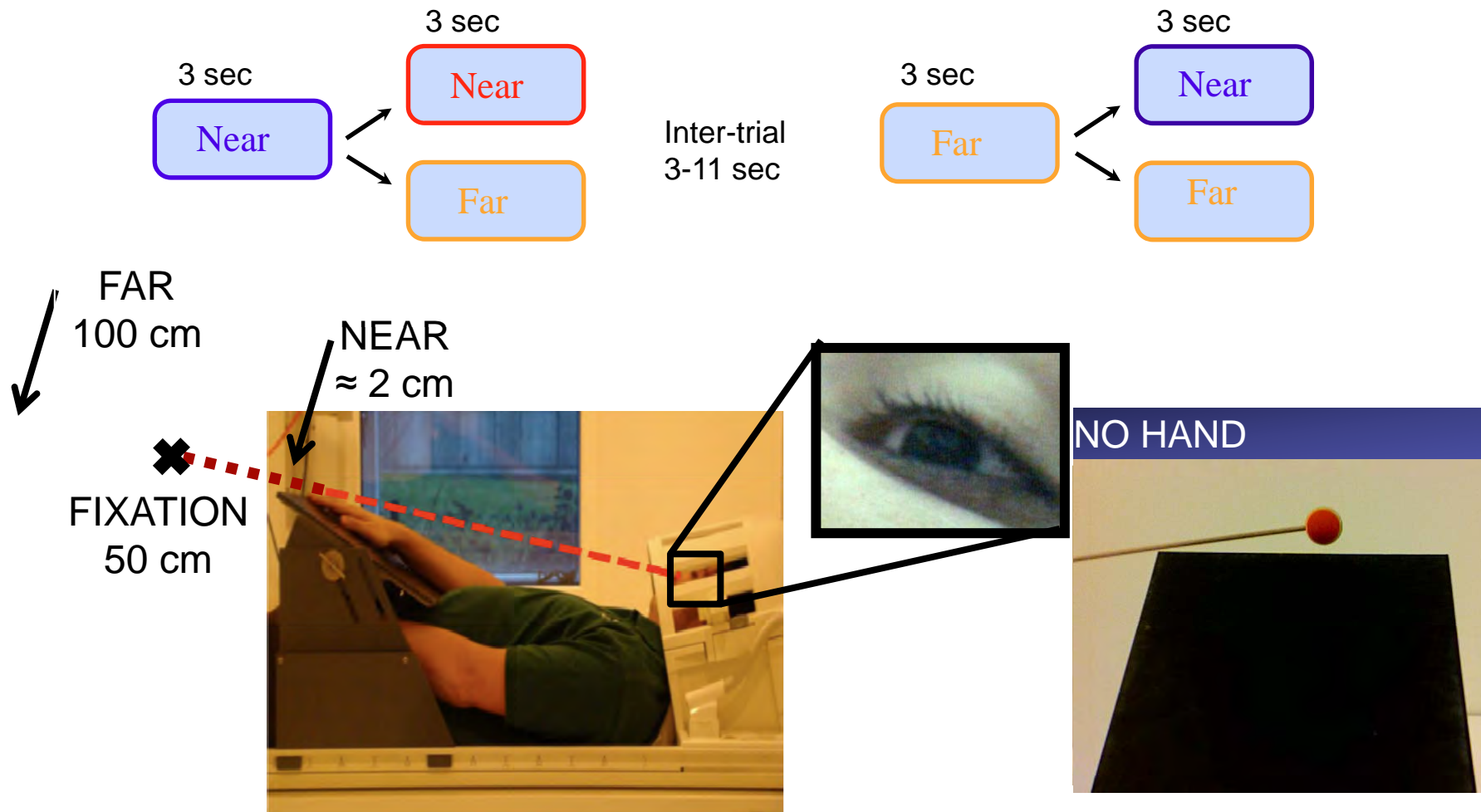


Gentile et al. (2010) J. Neurophysiol

Human premotor and intraparietal cortices performs multisensory integration

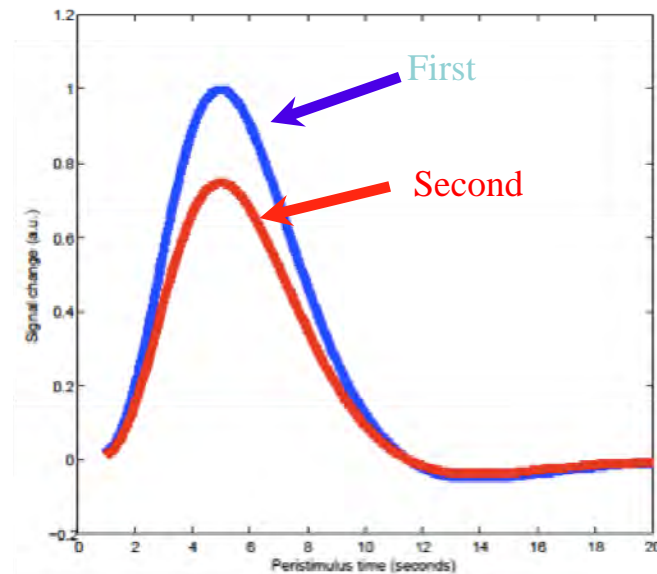
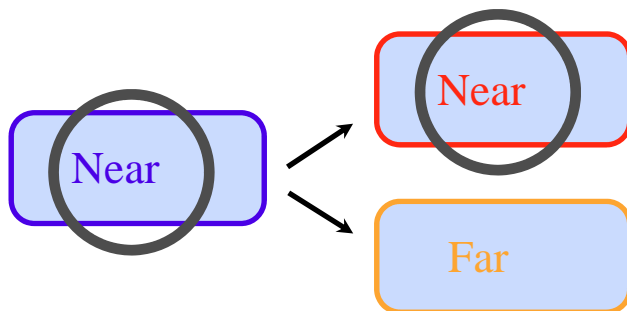


fMRI evidence for peripersonal space in human premotor and intraparietal cortices



Brozzoli et al. (In manuscript)

fMRI-adaptation evidence for peripersonal space in human premotor and intraparietal cortices



Brozzoli et al. (In manuscript)

fMRI-adaptation evidence for peripersonal space in human premotor and intraparietal cortices



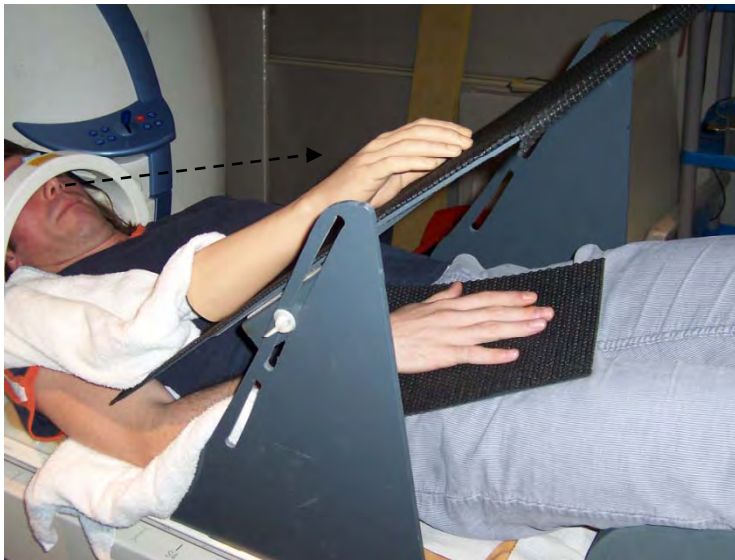
Brozzoli et al. (In manuscript)



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4. Imaging illusions of body ownership

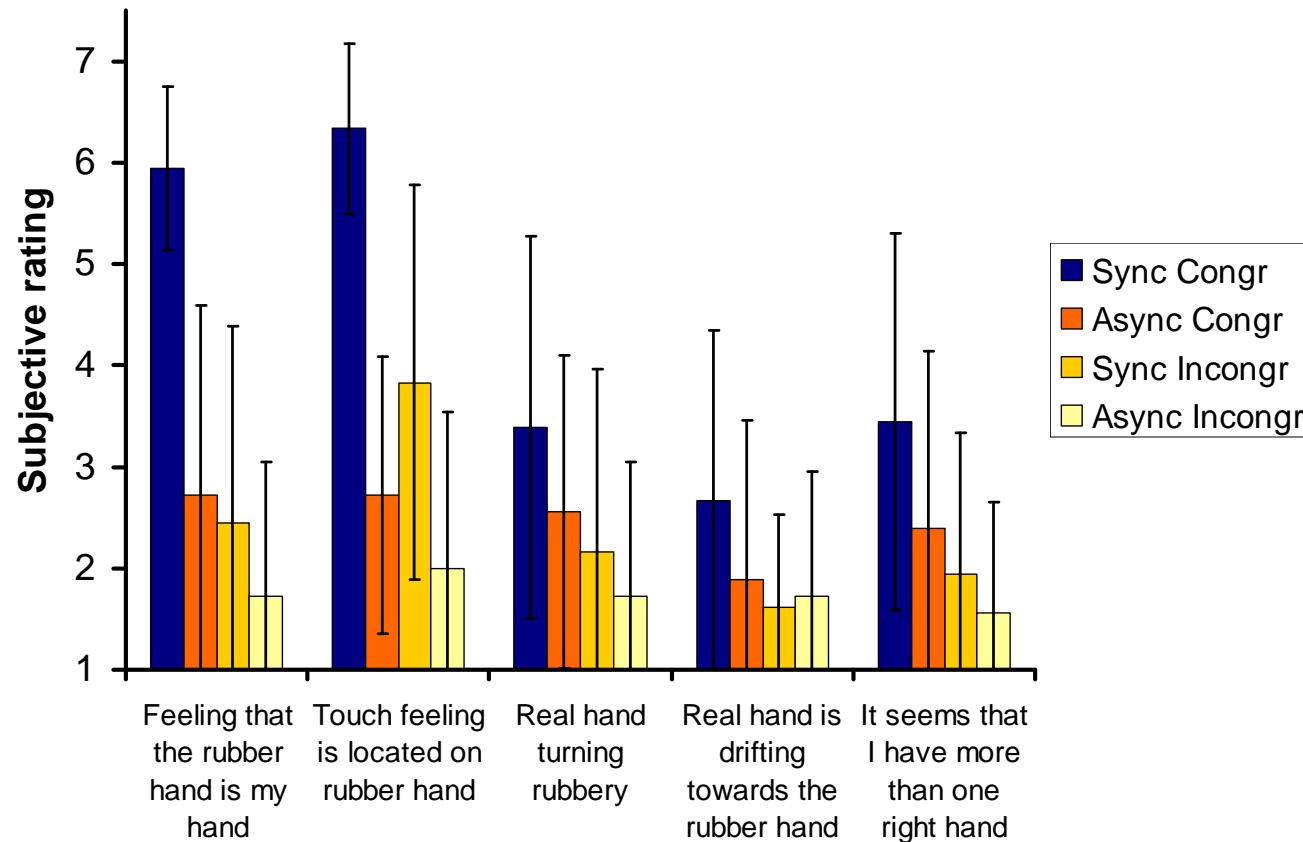
fMRI of rubber hand illusion



		Timing of brushstrokes	
		<i>Asynchronous</i>	<i>Synchronous</i>
Arm orientation	<i>Incongruent</i>	Asynch. Incongr.	Synch. Incongr.
	<i>Congruent</i>	Asynch. Congr.	Synch. Congr.

Ehrsson et al. (2004) *Science*

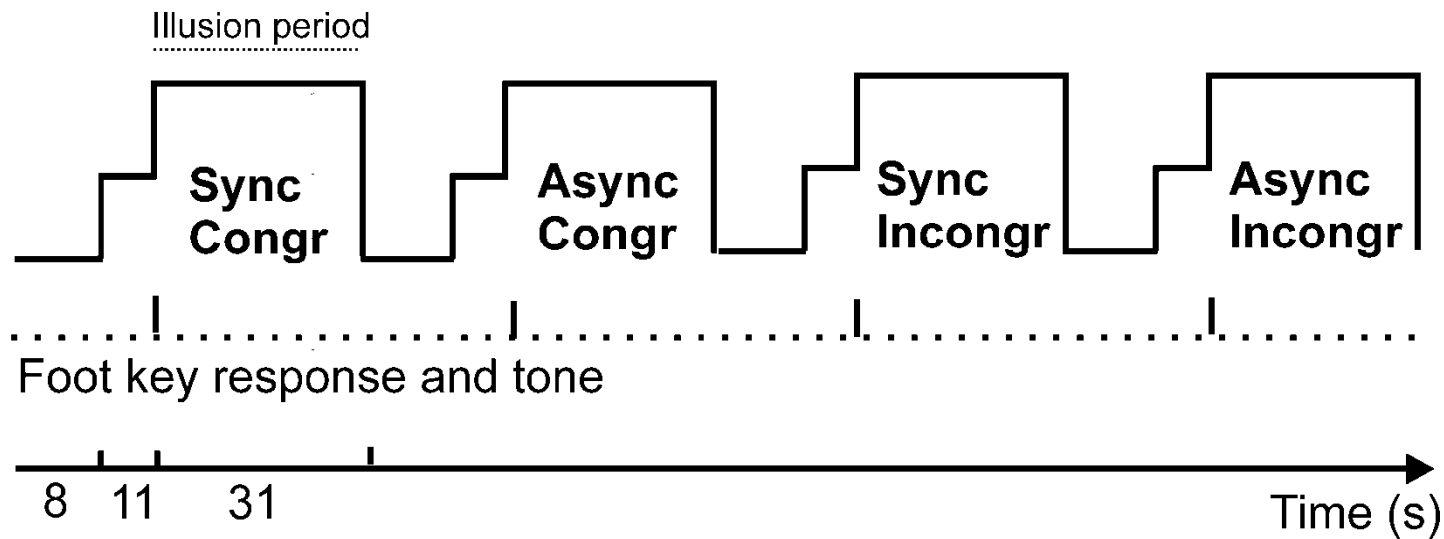
Illusion ratings



Interaction brushstroke-timing and arm orientation
($F(1, 17)=14.22$; $p<0.005$)

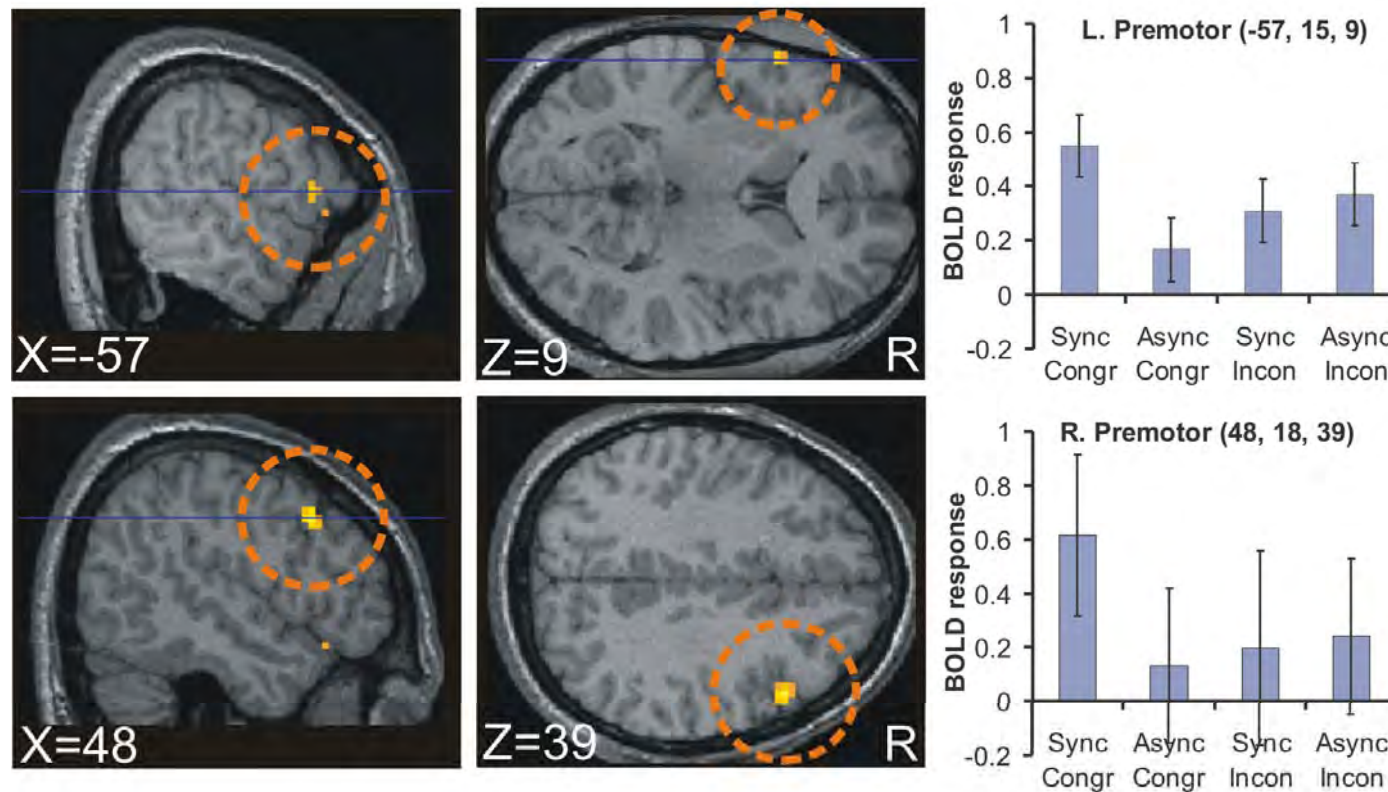
Ehrsson et al. (2004) *Science*

Experimental paradigm



Ehrsson et al. (2004) *Science*

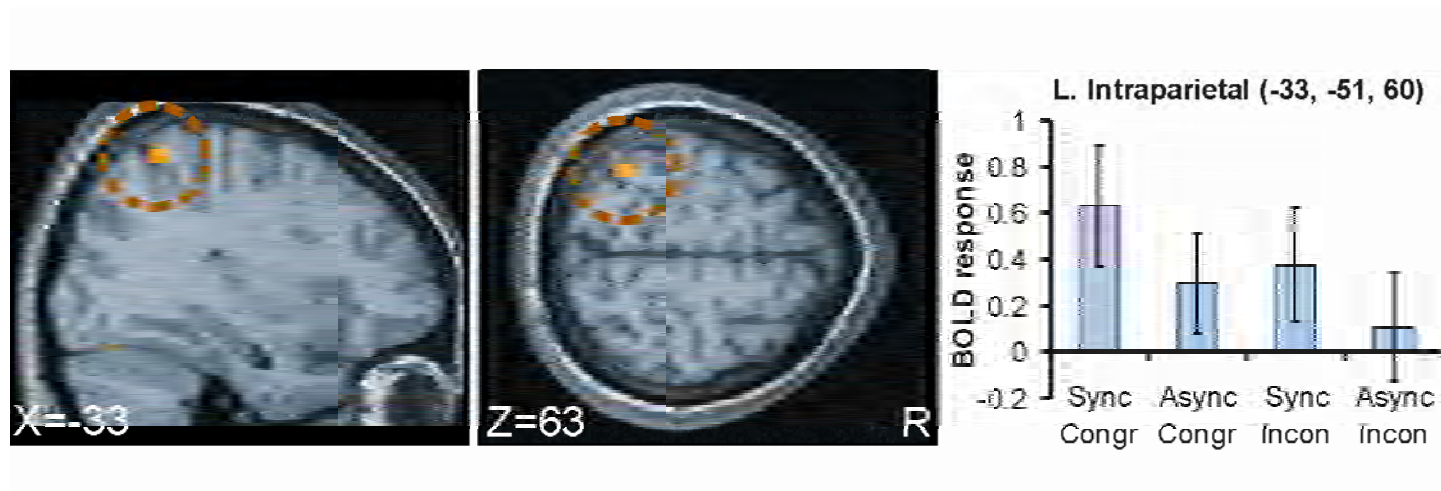
Premotor activity reflects feeling of ownership (superadditive effect)



Left and right ventral premotor cortex ($p < 0.05$ corrected)

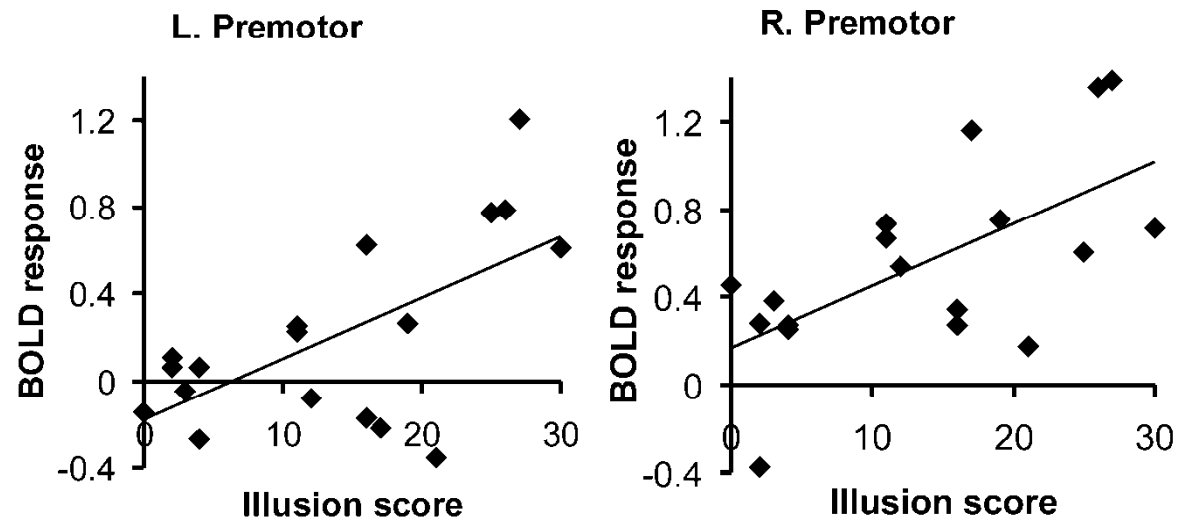
Ehrsson et al. (2004) *Science*

Parietal activity reflects congruent hand position and synchrony (additive effect)



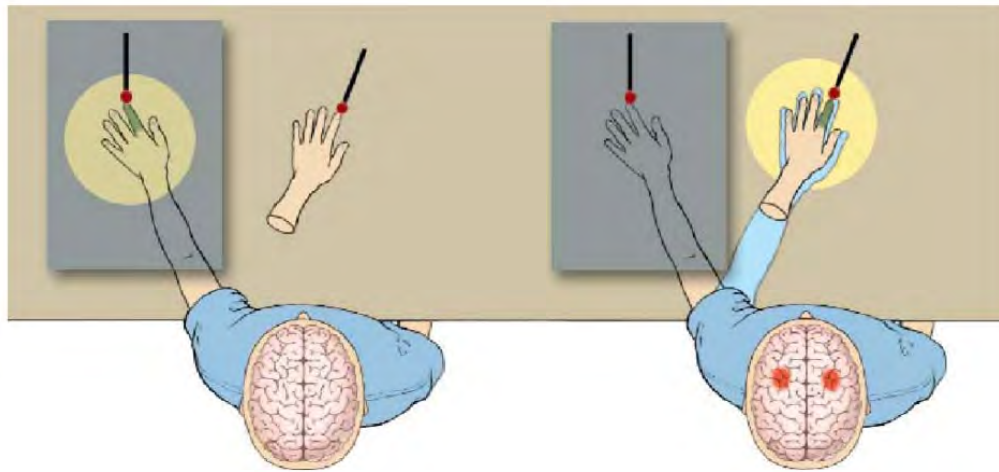
Conjunction of main effects of synchrony and anatomical congruency ($p < 0.001$ corrected)

Correlation between illusion ratings and premotor activity

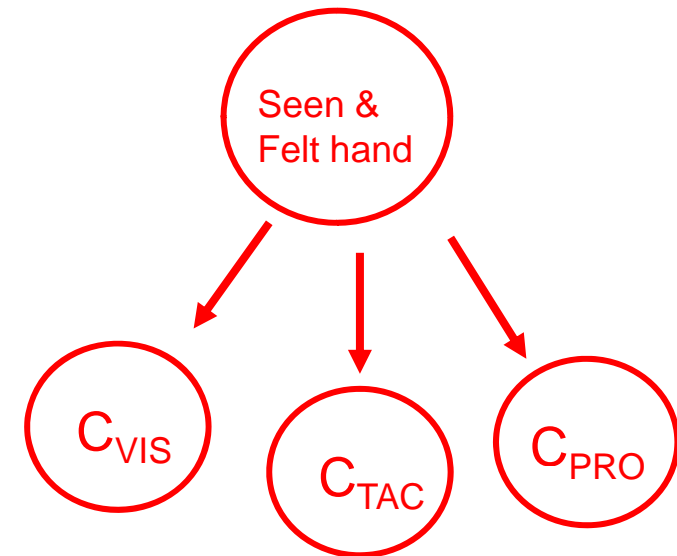


Ehrsson et al. (2004) *Science*

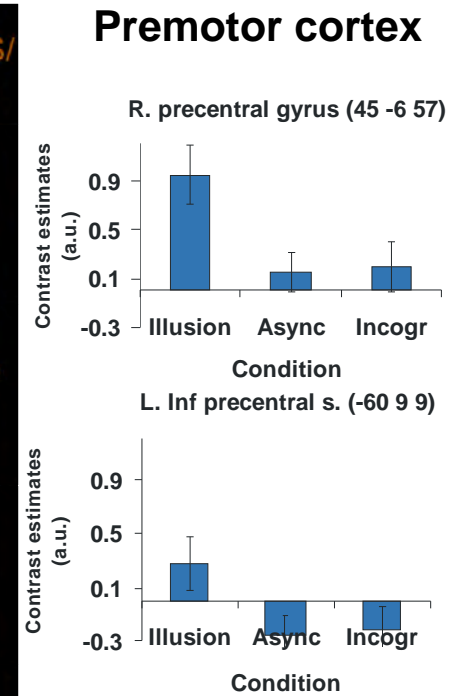
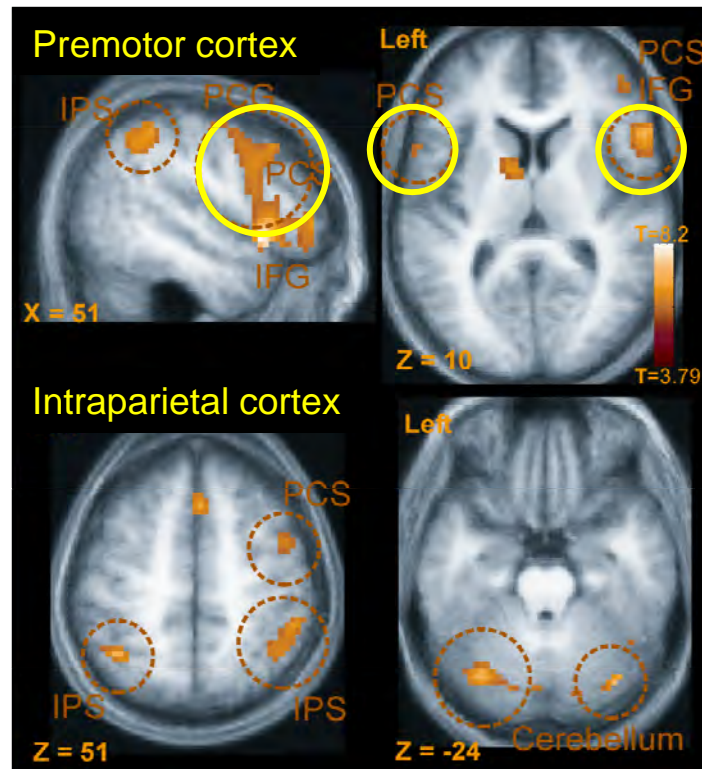
Conclusion: multisensory integration in premotor and intraparietal areas reflect limb ownership



Botvinick (2004) *Science*

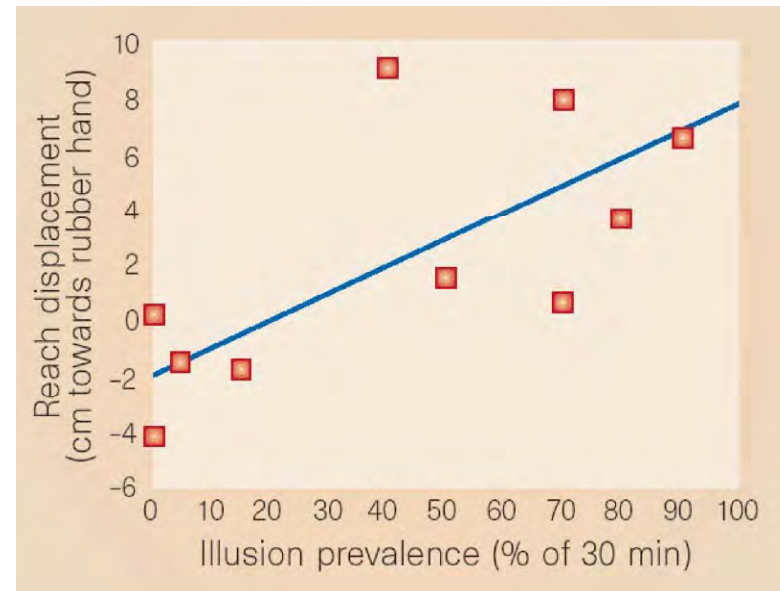


Somatic rubber hand illusion



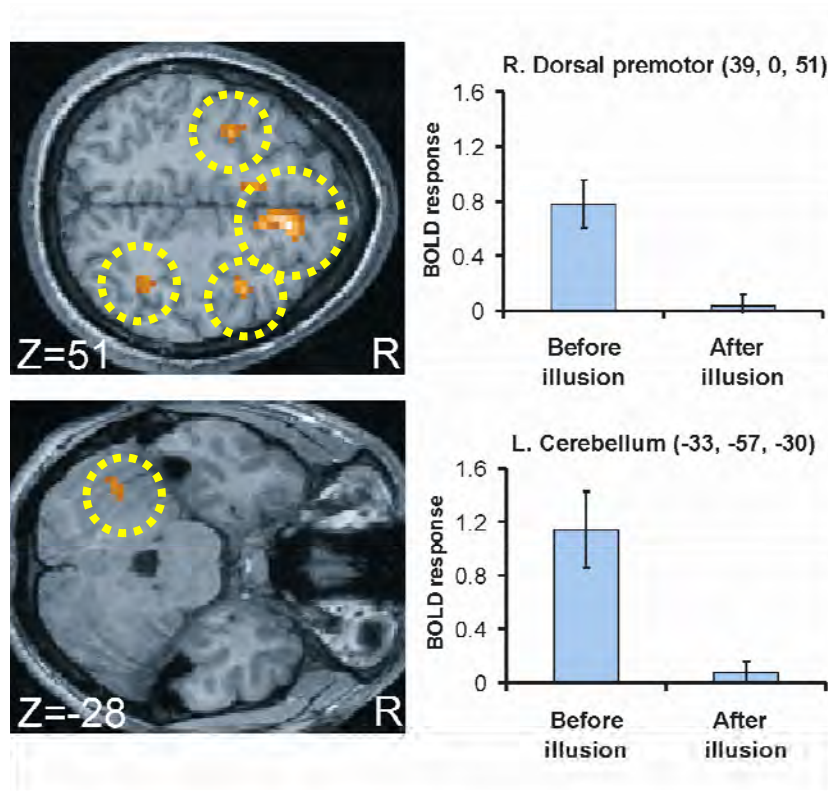
Ehrsson et al. *J Neurosci.* 25:10564-73, 2005

Re-calibration of position sense



Botvinick and Cohen (1998) *Nature*

Recalibration of position sense in a 'reaching circuit' before illusion onset



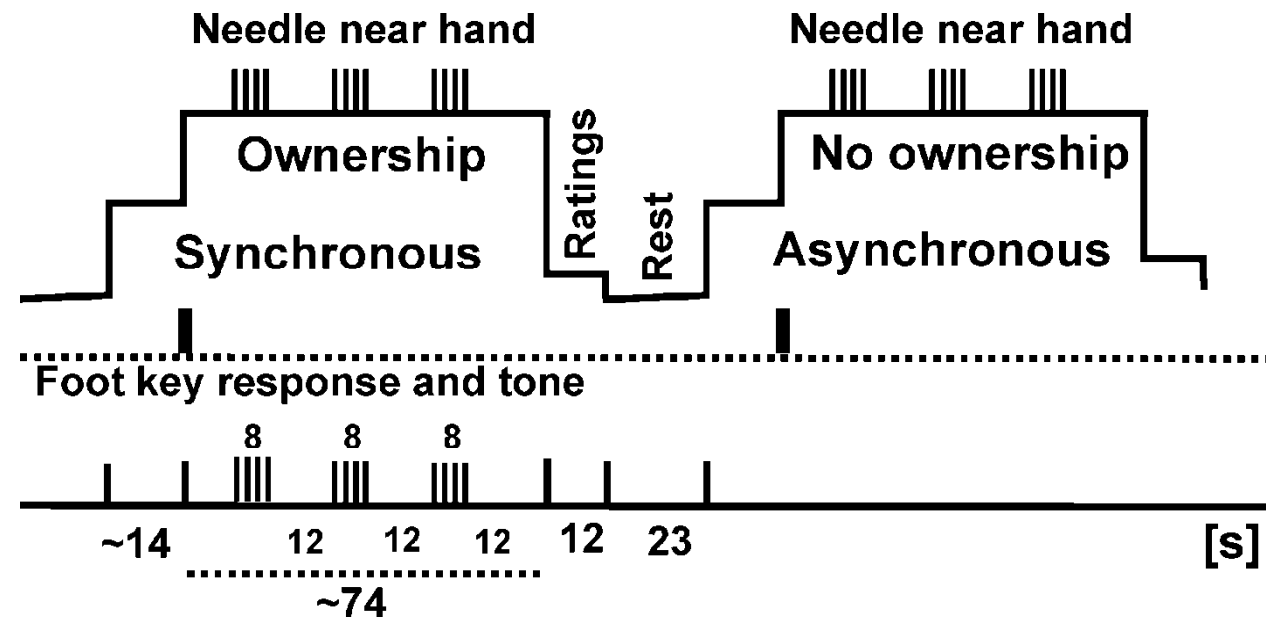
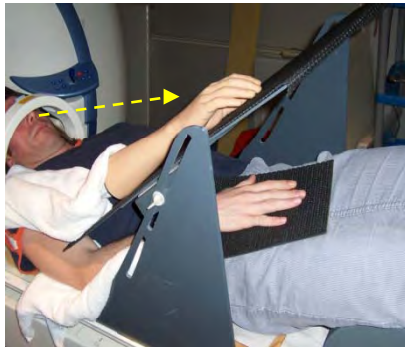
Supplementary motor area, dorsal premotor cortex, the posterior parietal cortex, and the cerebellum

Ehrsson et al. (2004) Science

Objective evidence by threatening the rubber hand

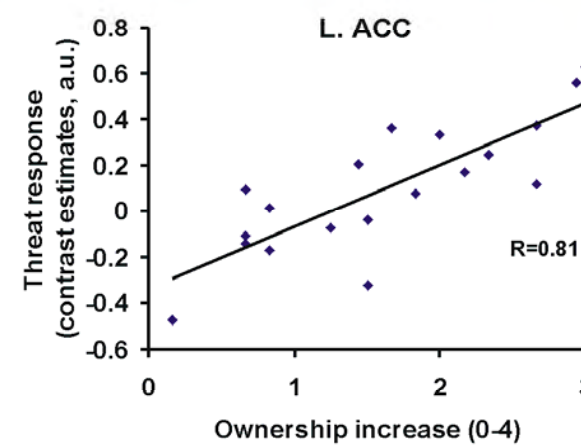
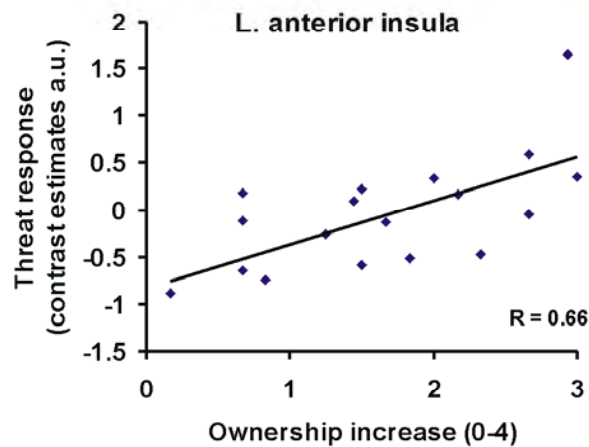
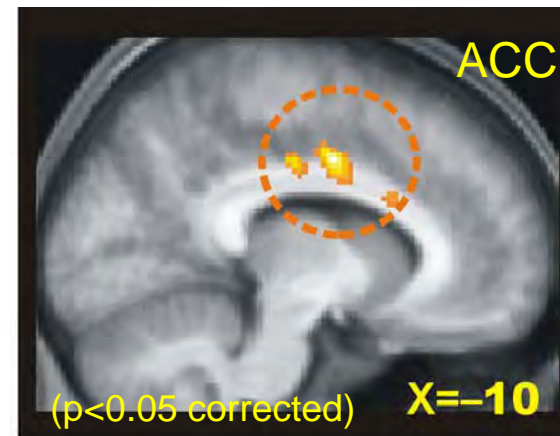
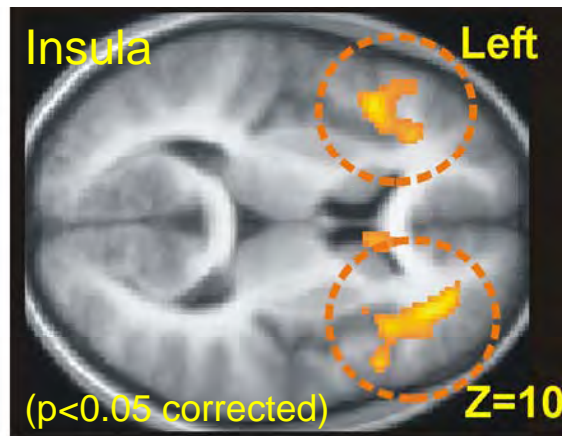


Experimental design



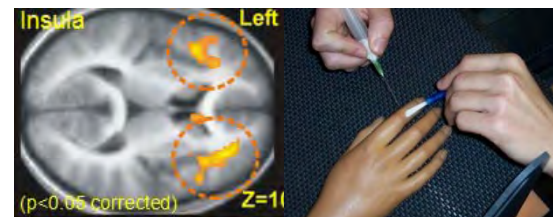
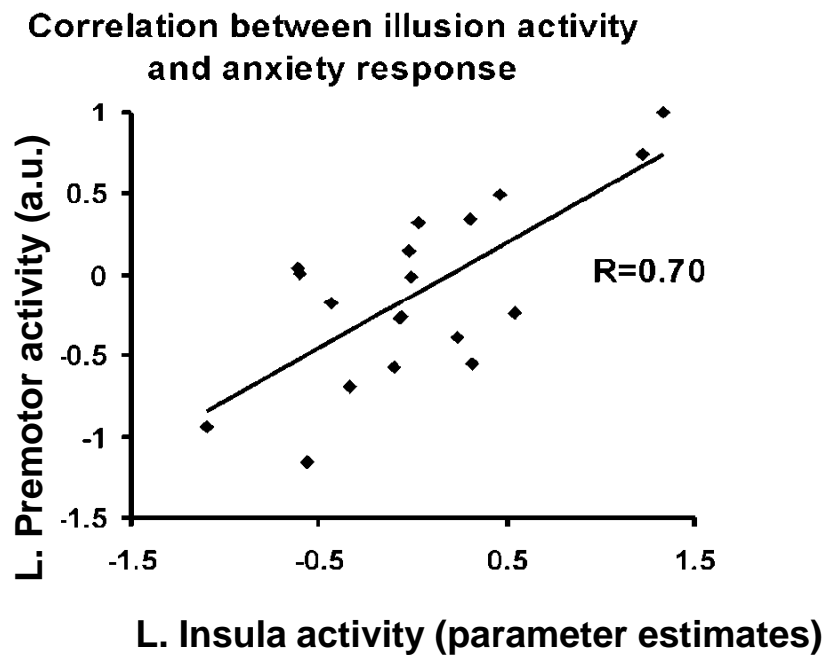
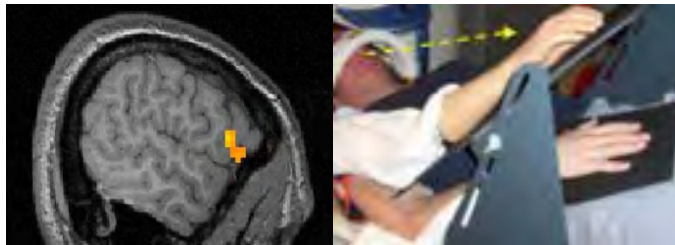
Ehrsson et al. (2007) *PNAS* 104:9828-9833

Increased threat-evoked response when owning the hand



Ehrsson et al. (2007) *PNAS* 104:9828-9833

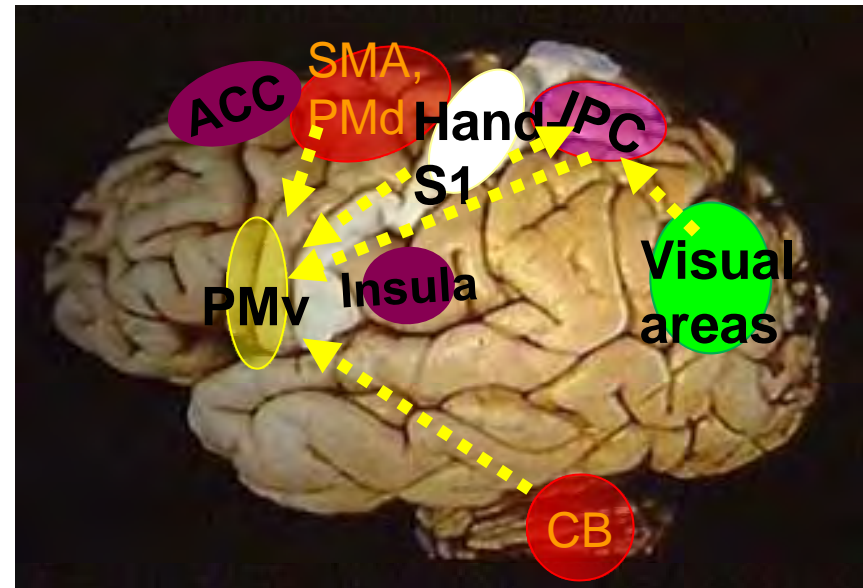
Activity in multisensory areas predict the threat-evoked response



Ehrsson et al. (2007) *PNAS*

A preliminary model of limb ownership

- Processing of visual and tactile signals in early sensory areas
- Integration of visual and tactile signals in posterior parietal cortex.
- Recalibration of position sense in motor regions.
- Match of temporally and spatially congruent multisensory signals in premotor cortex (PMv) produce ownership
- Changes in other brain systems, e.g. in the emotional system

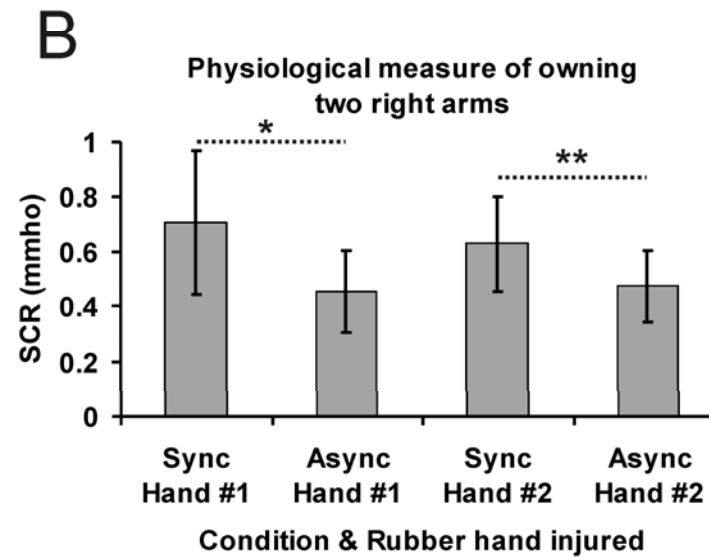


Three-arm-illusion: a remarkable case of construction



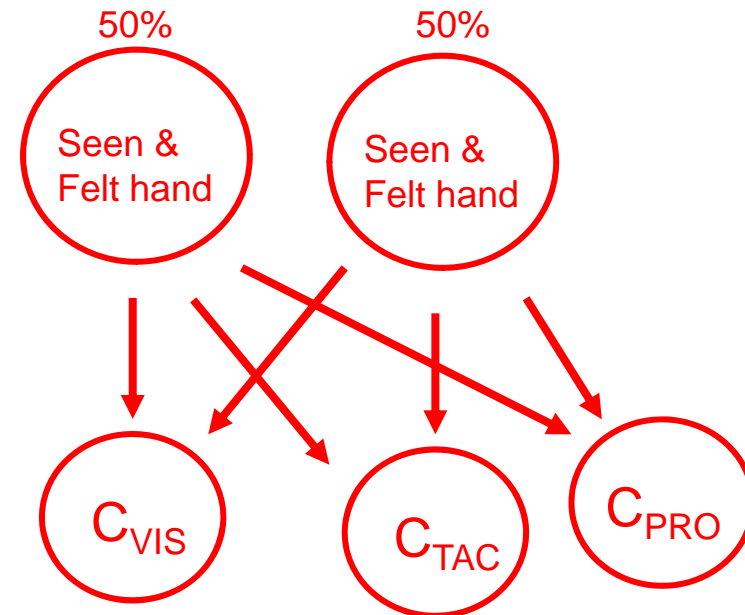
Ehrsson (2009) *Perception* 38, 310-312

Objective evidence



Ehrsson (2009) *Perception* 38, 310-312

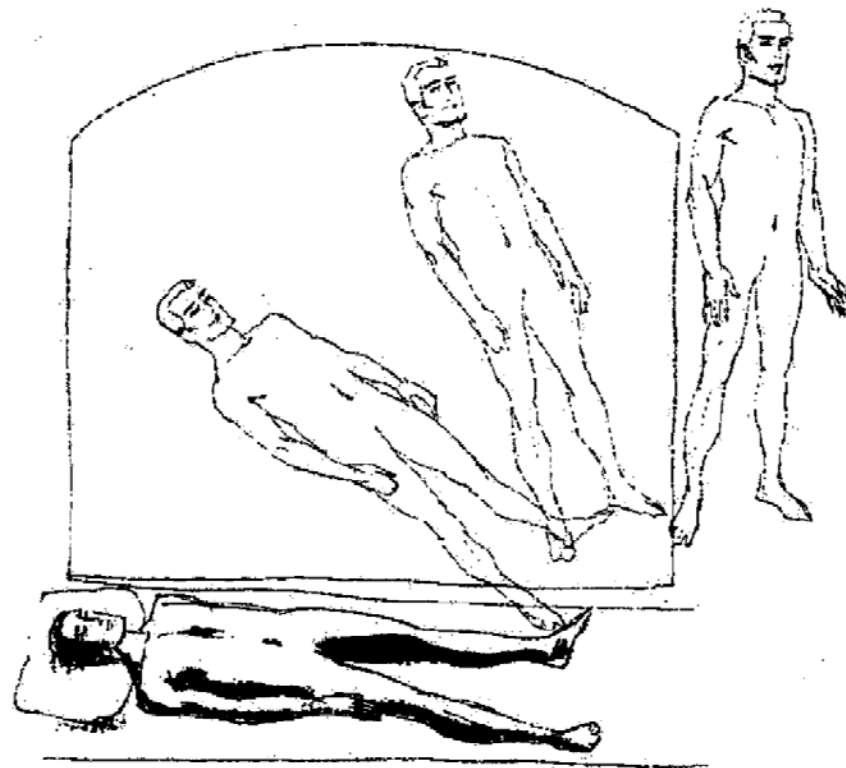
Three-arm-illusion: a remarkable case of construction



9 februari 2011

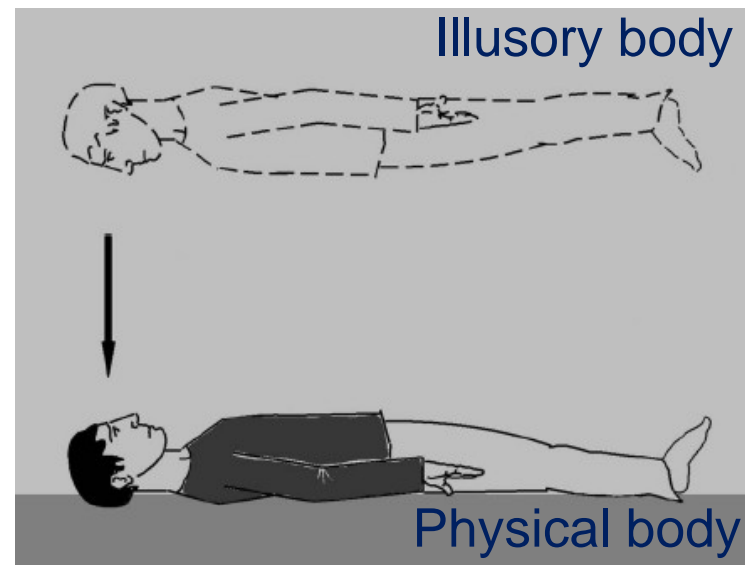
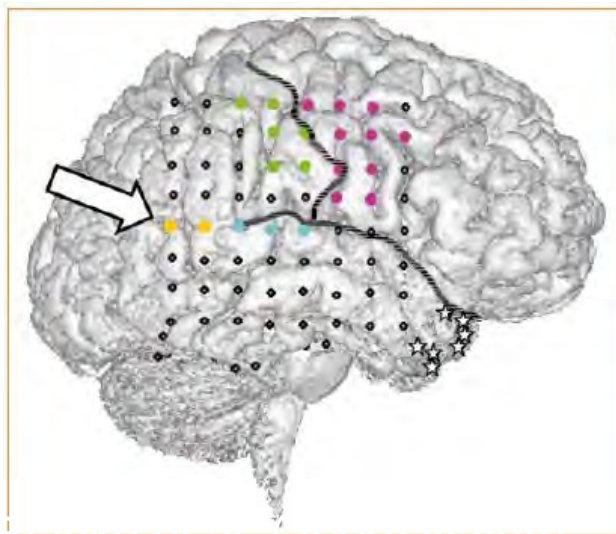
Ehrsson (2009) *Perception* 38, 310-312

5. Extending the model to ownership of entire bodies



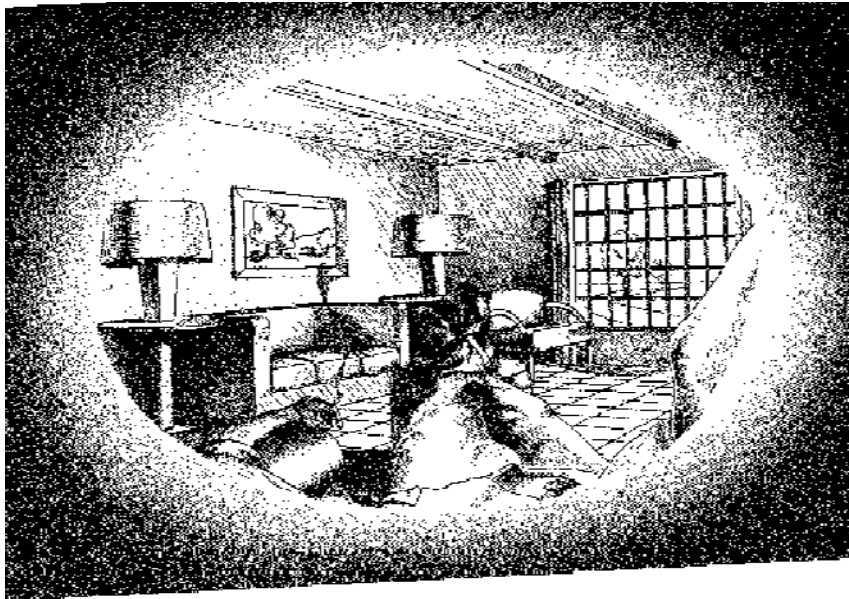
Out-of-body experiences (From Brugger 2002)

Neurological out-of-body experiences

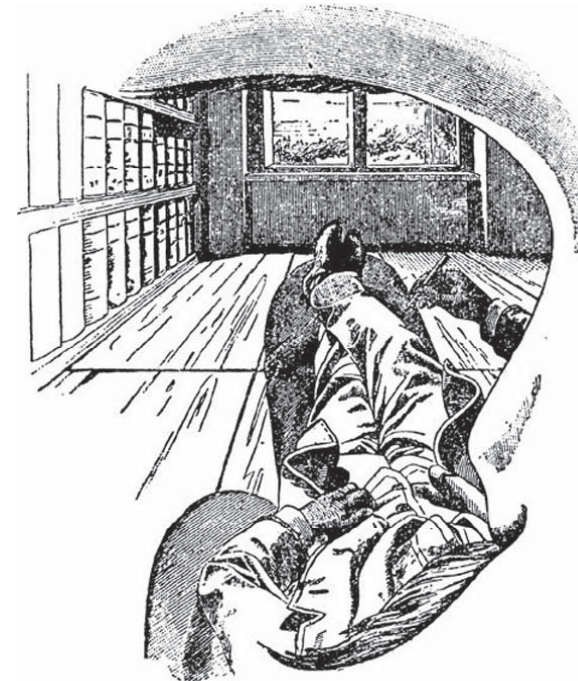


Blanke et al. (2002) *Nature*; Blanke and Mohr (2005) *Brain Res. Reviews*

First-person perspective and body ownership



Gibson (1972) *The ecological approach to visual perception* (1972)



Ernst Mach (1885)
Analyse der Empfindungen

Out-of-body illusion



Ehrsson (2007) *Science* 317: 1048

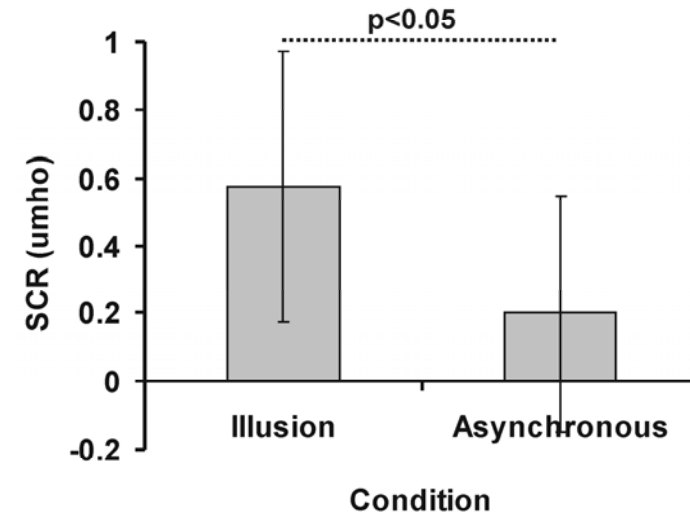
Experimental evidence

A



BBC
TWO horizon

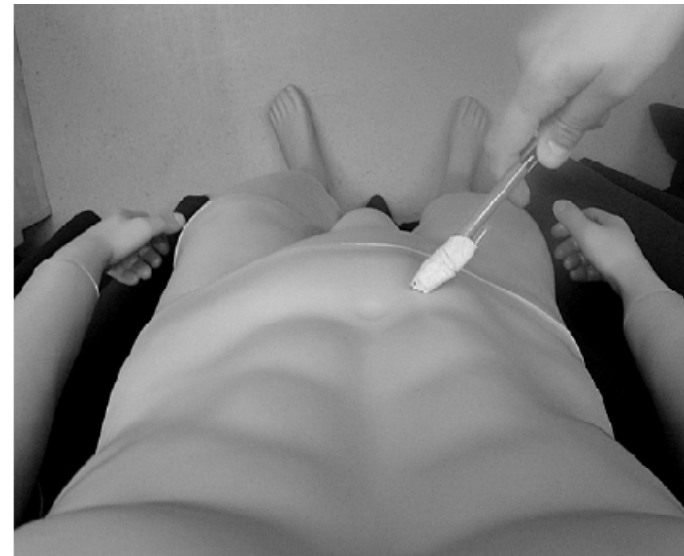
B



Registration of skin conductance response (SCR)

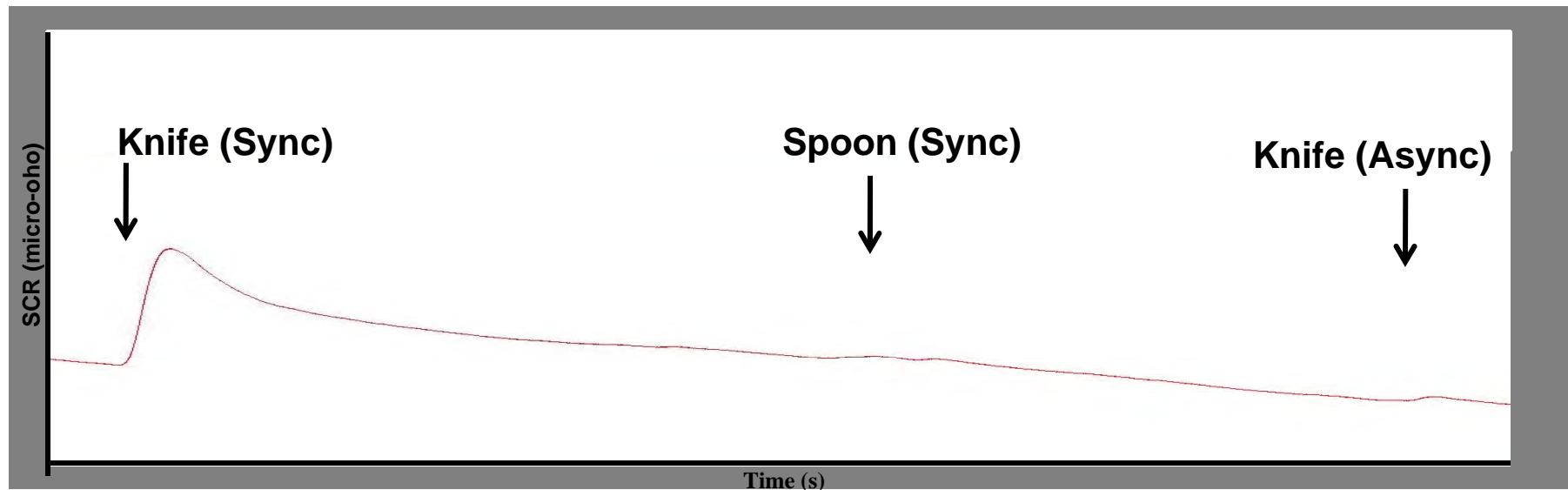
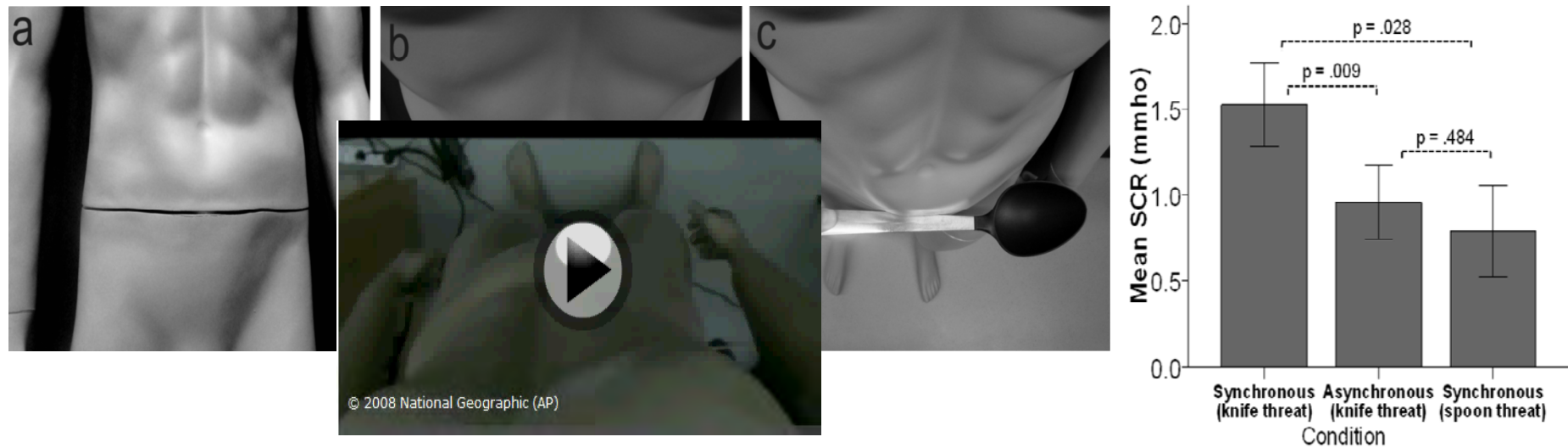
Ehrsson (2007) *Science*

Ownership of an entire body other than oneself



Petkova & Ehrsson et al. PLoS One (2008)

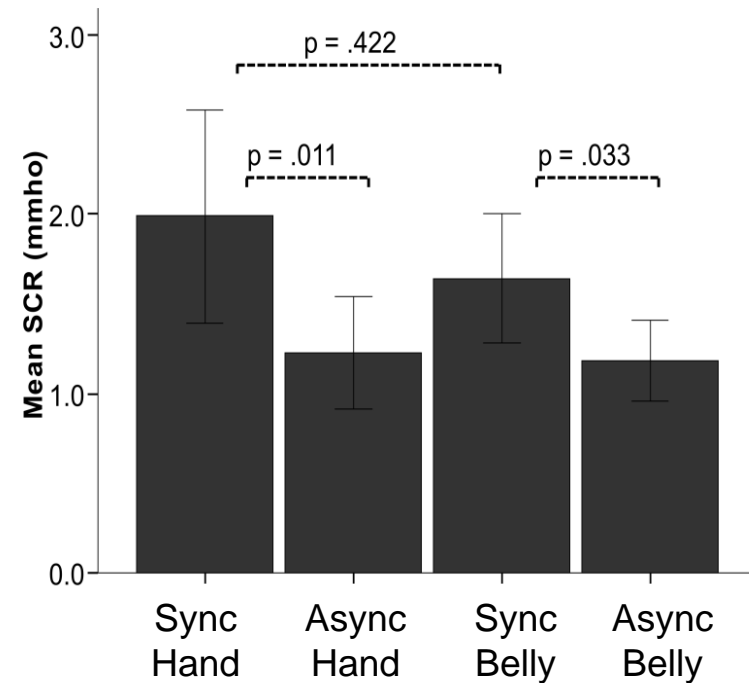
Objective test: Skin Conductance Response



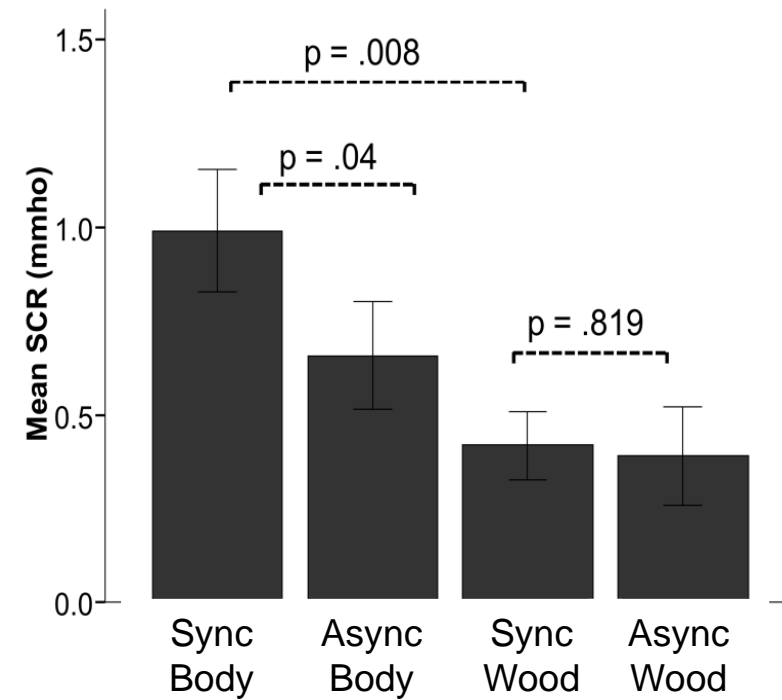
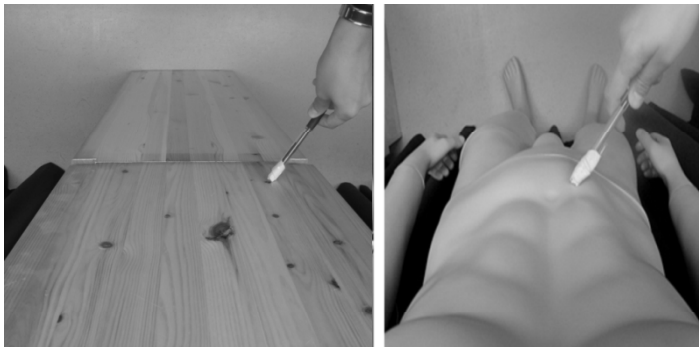
Generalization of ownership to non-stimulated body parts

Key experimental test:

1. Brush hand → 2. Cut Belly



Effect of humanoid body shape



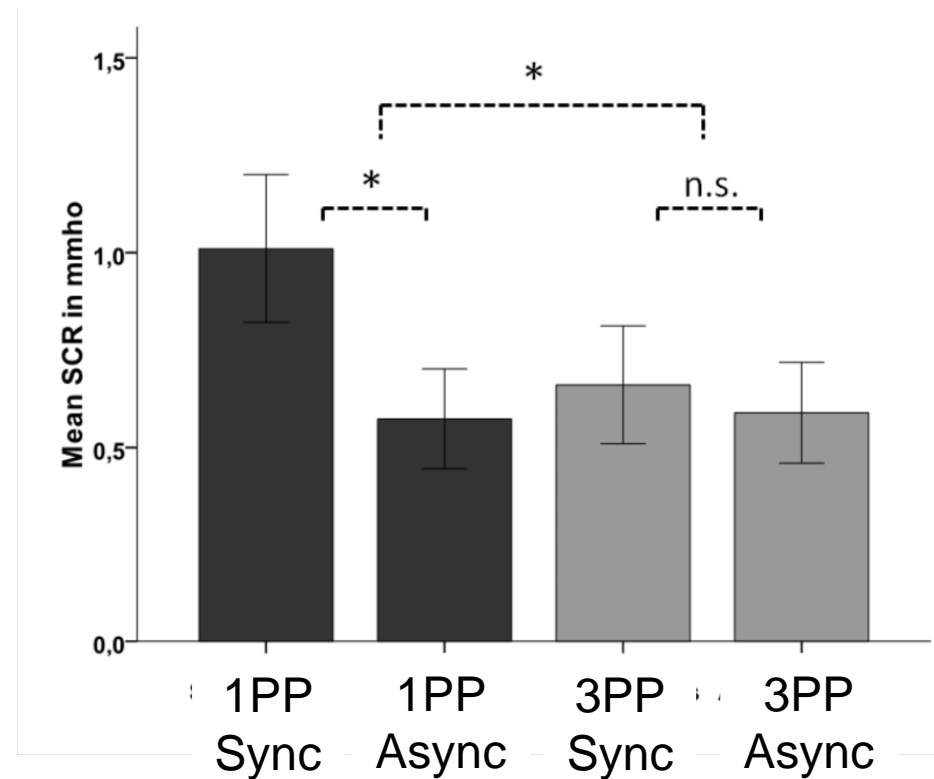
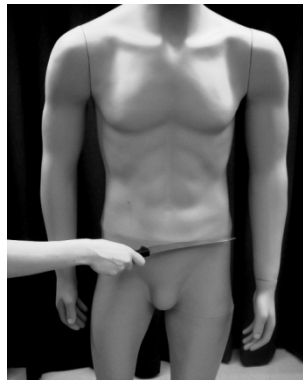
Petkova & Ehrsson PLoS One (2008)

Effect of visual perspective

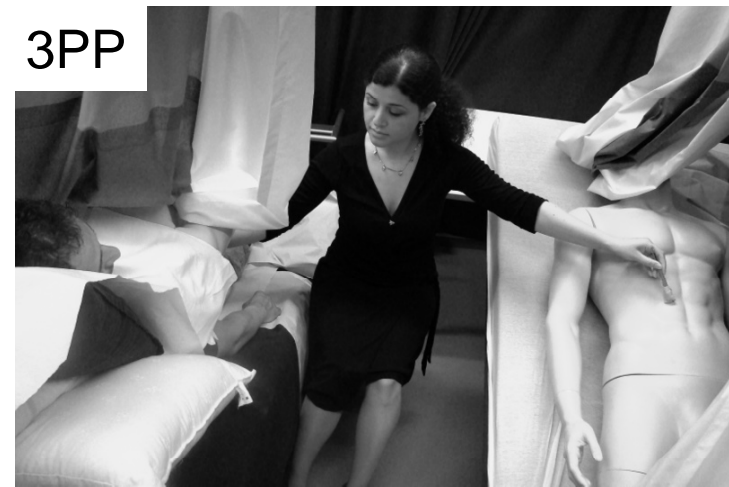
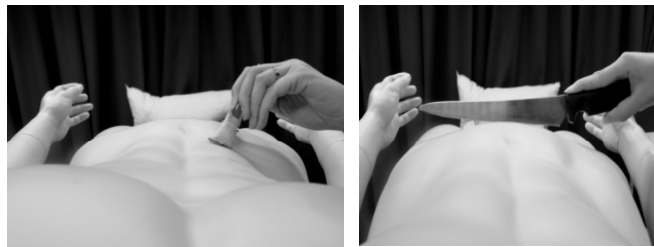
First-person-
perspective
(1PP)



Third-person-
perspective
(3PP)

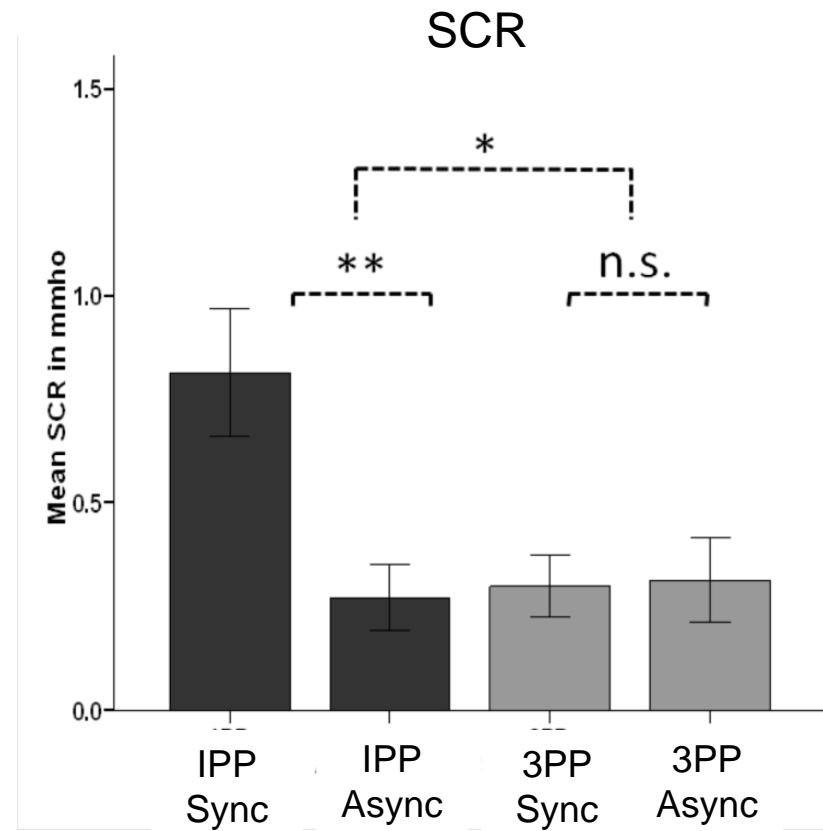


The illusion can be induced without video-technology, but only from the first-person perspective



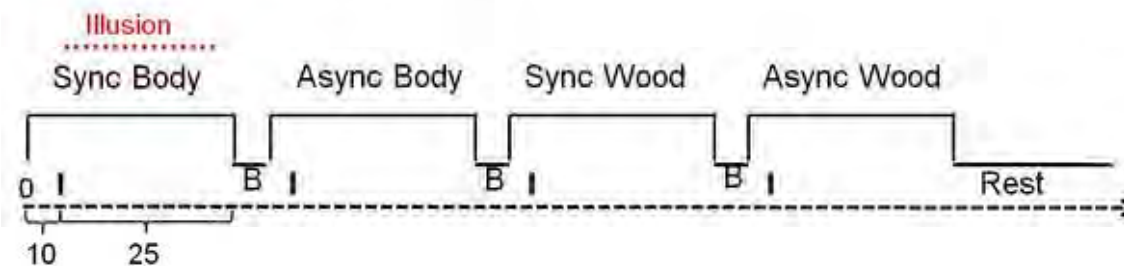
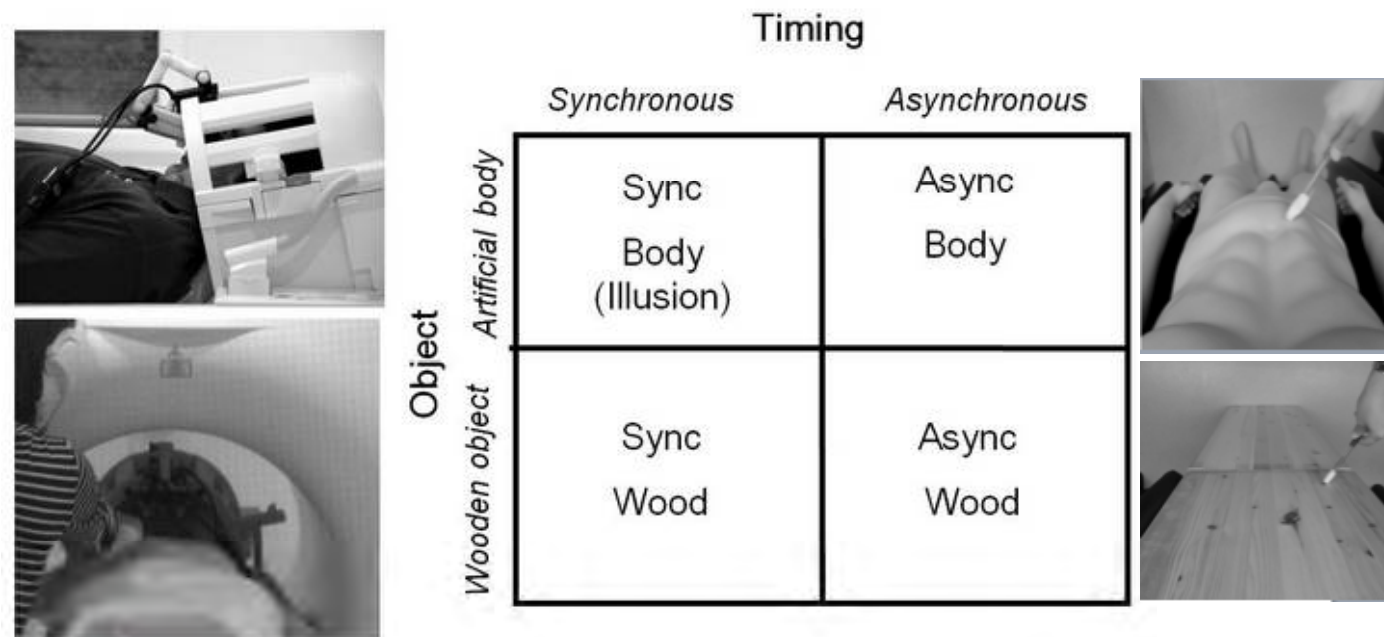
Petkova et al. *In revision Frontiers in Cognition*

The illusion can be induced without video-technology, but only from the first-person perspective



Petkova et al. *In revision Frontiers in Cognition*

Imaging the full-body illusion: Object x Timing



Petkova et al. (submitted)

Interaction effect (Body X Sync)



Imaging the full-body illusion: Perspective x Timing

		Timing	
		<i>Synchronous</i>	<i>Asynchronous</i>
Perspective	Third PP	Sync 1-PP	Async 1-PP
	First PP	Sync 3-PP	Async 3-PP



Petkova et al. (submitted)

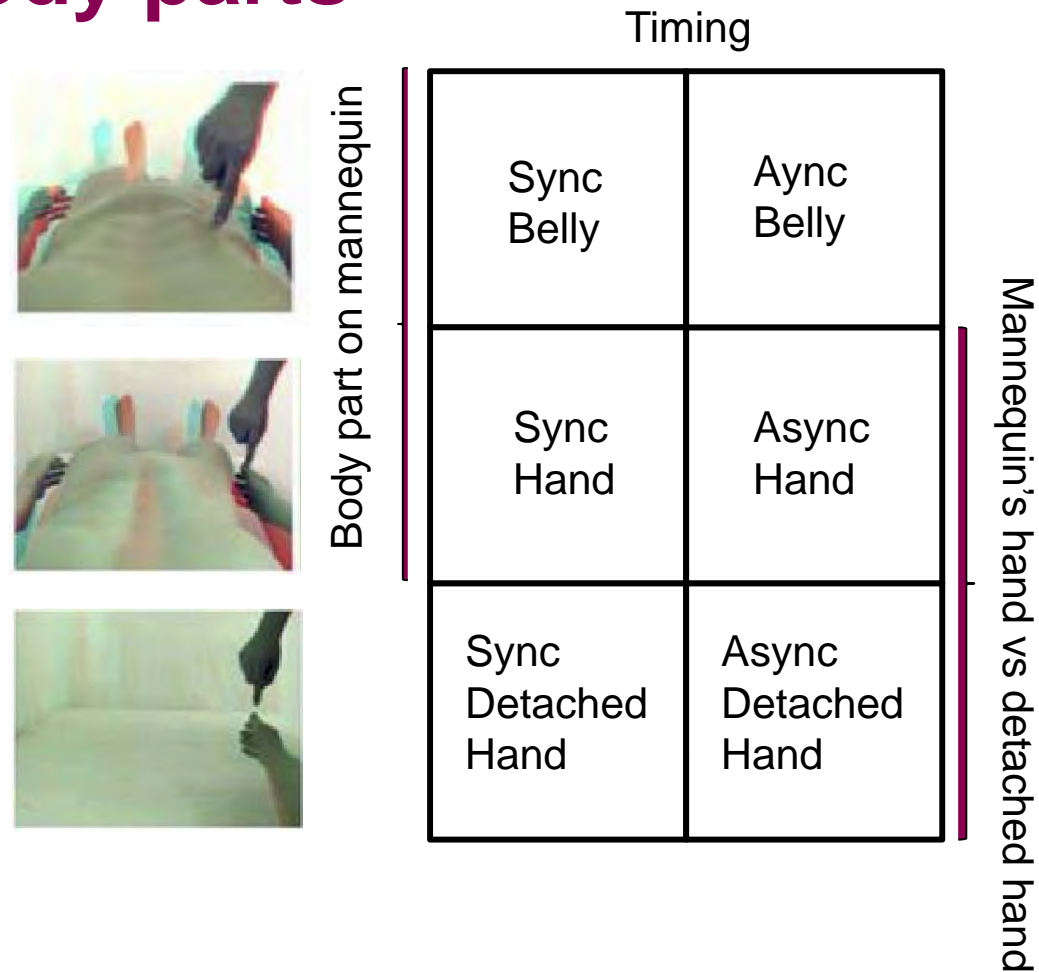
Interaction effect (1PP X Sync)



Correlation between illusion strength and interaction BOLD effect



Imaging the full-body illusion: Generalisation of ownership across body parts

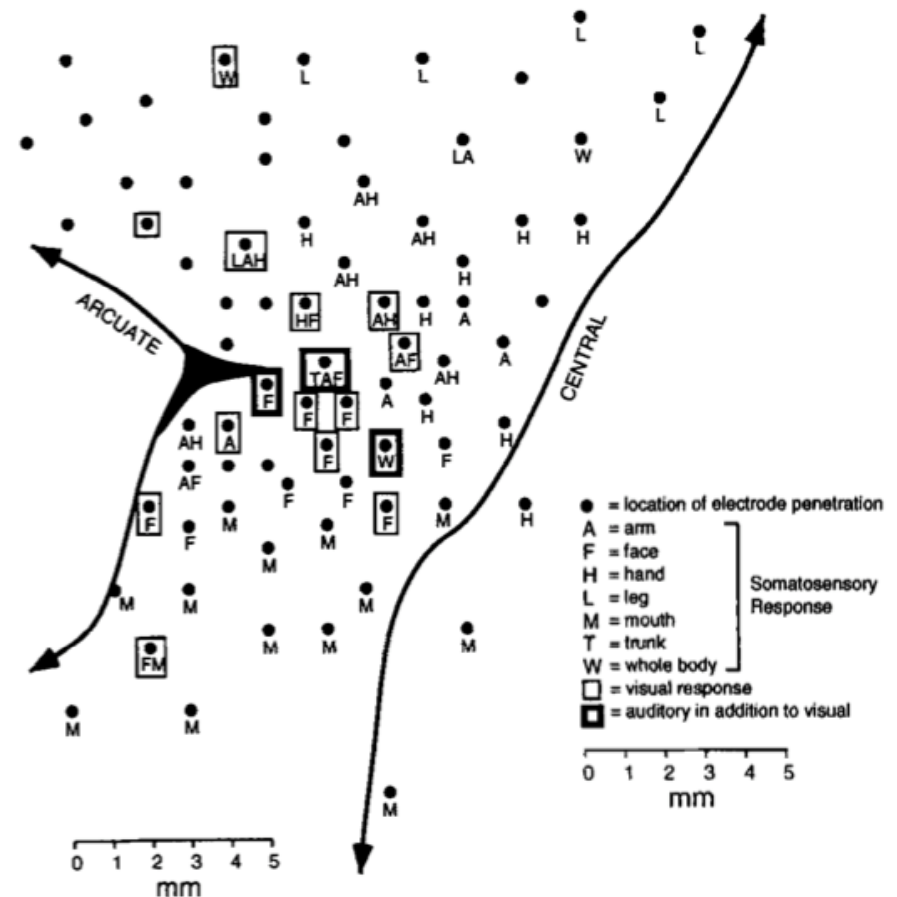


Petkova et al. (submitted)

Body-part specific and body-part general activations



Body-part specific and body-part general activations



Petkova et al. (submitted)

Graziano et al. (2000) Exp Brain Res

Hand attached to mannequin Vs detached hand (interaction effect)

Generalization of ownership between body-specific sections

Interaction (manniquin's hand / detached hand X Timing)

Interim conclusion: ownership of entire bodies

- Visual information from the **first-person perspective**, in conjunction with **spatially and temporally congruent tactile, proprioceptive and visual signals** in **ego-centric reference frames** are *necessary and sufficient* factors elicit a sense of ownership of an entire body.
- Our fMRI results suggest that the key neural mechanism is the **integration of visual and somatic signals in body-part-centred reference frames** by **multisensory neuronal populations** in **premotor and intraparietal cortex**.
- Importantly, these **multisensory mechanisms operate in parallel** for different body parts with **functional interplay between these processes**.

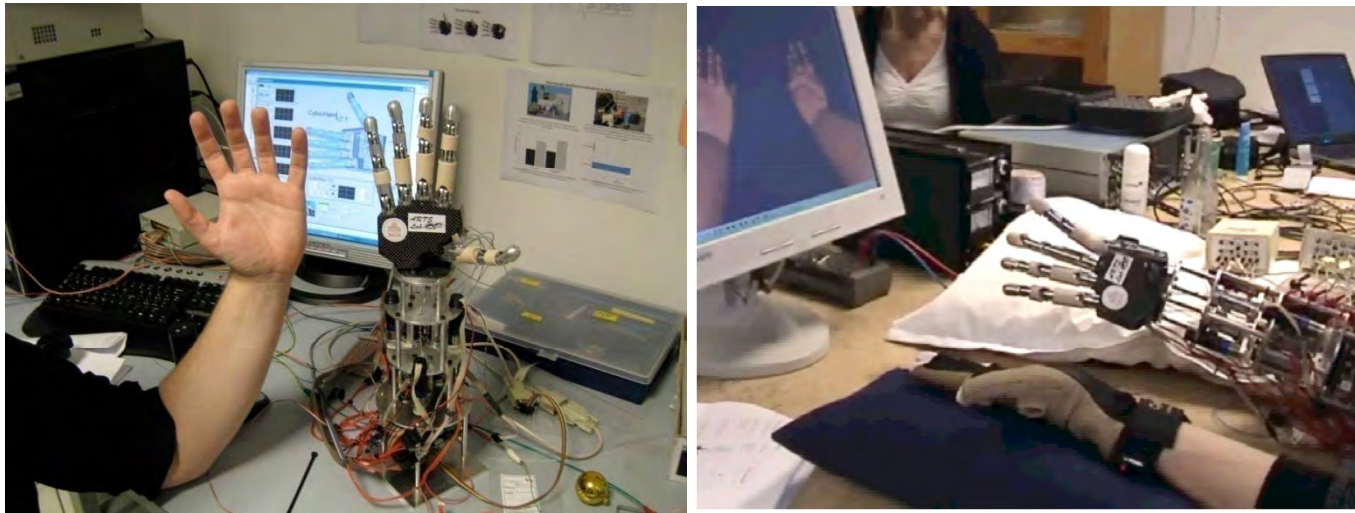
6. Applications: simulated bodies and advanced prosthetics

Projecting ownership to virtual bodies



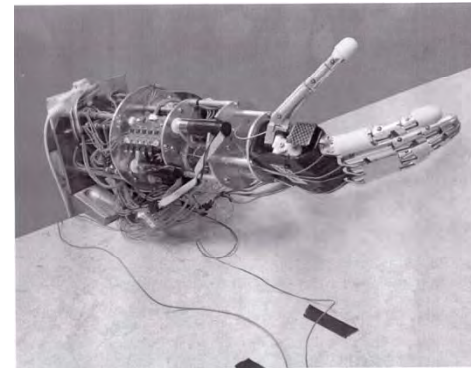
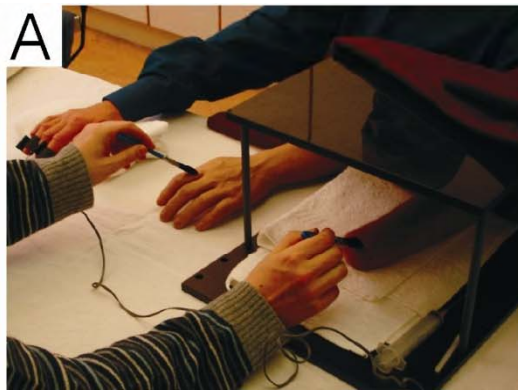
- Slater et al. (PLOS ONE 2010)
- Jesper Mortensen, Pankaj Khanna, Insu Yu, Bernhard Spanlang, Mel Slater EPSRC 'Presence in the Virtual Light Field' and FET PRESENCIA.

Humanoid robotic hand prostheses

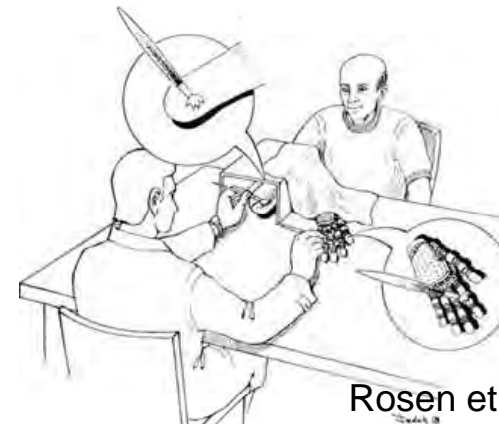


- SMART hand project (6FP project coordinated from University of Lund; Fredrik Sebelius Dept. Electrical Measurements, Lund University)
- “the PISA hand” - developed and provided by the ARTS Lab, Scuola Superiore Sant’Anna (IST-2001-35094)

Upper limb amputees can be induced to experience a rubber hand as their own

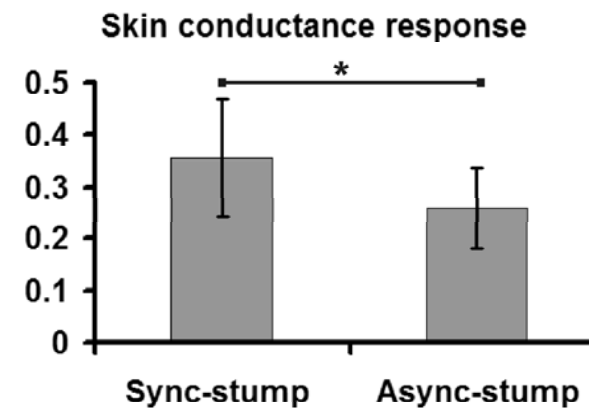
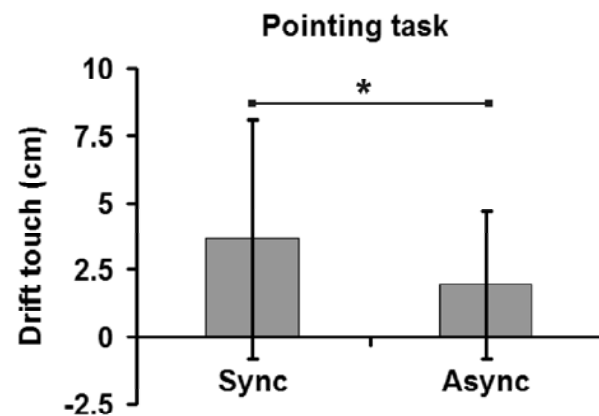
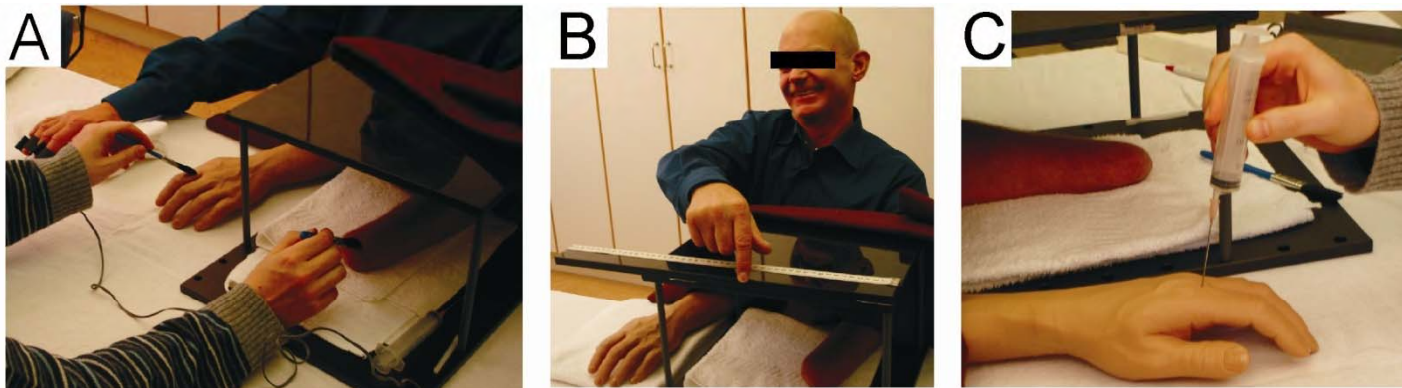


Ehrsson HH, Rosén B, Stocksélius A, Ragnö C,
Köhler P, Lundborg G (2008) *Brain* 131, 3443-3452



Rosen et al. (2009) *Scand J
Plast Reconstr Surg Hand
Surg.* 43:260-266

Upper limb amputees can be induced to experience a rubber hand as their own



Ehrsson et al. (2008) *Brain* 131, 3443-3452

Summary



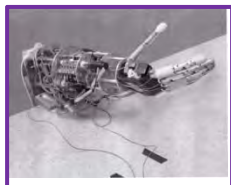
- The problem of body ownership can be explained within a multisensory framework.



- The natural constraints of the rubber hand illusion and full-body illusions obey multisensory integration principles.



- Activity in premotor and intraparietal cortex obeys the ‘multisensory rules’ of the body ownership illusions; thus multisensory integration in body-part-centered coordinates is a likely mechanism of ownership.



- By employing the multisensory principles of body ownership one can create a new type of arm-prosthesis that feels more like a real limb.

Brain, Body and Self Laboratory



Dr. Alexander Skoglund, research engineer



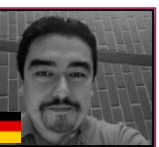
Dr. Hiske van Duinen, postdoc



Dr. Claudio Brozzoli, postdoc



Dr. Loretxu Bergouignan, postdoc



Dr. Laura Schmalzl, postdoc



Valeria Petkova, PhD student.



Giovanni Gentile, PhD student

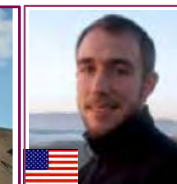


Andreas Kalckert, PhD student.



Arvid Guterstam PhD student

Björn van der Hoort, Hedvig Zetterberg and Chris Berger (master students)



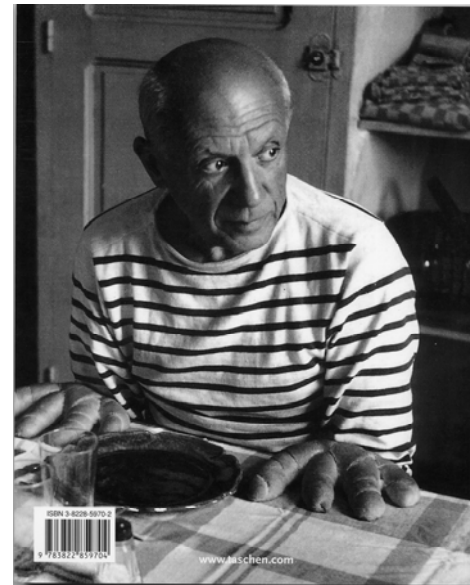
JAMES S. McDONNELL FOUNDATION



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<http://www.neuro.ki.se/ehrsson/>
Postdoc positions open!

Thank you!



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