Mirror neurons seem to bridge the gap between one agent and another; to represent 'my action' and 'your action' in the same way.

Heyes, 2010

Where Do Mirror Neurons Come From?

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Origins

- Mirror neurons are an adaptation (Adaptation Hypothesis)
- Mirror neurons are the result of associative learning (Associative Learning Hypothesis)
- Some combination of the two

Origins (cont)

- Mirror neurons are an adaptation (Adaptation Hypothesis)
  - A characteristic that evolved to fulfill a particular function
  - Adaptations solve a specific problem in an efficient, reliable and precise way, in this case, for understanding the actions of others
  - genetic evolution produced mirror neurons, and they were favored by natural selection because they supported action understanding
  - Therefore, monkeys and humans are born with MNs
- In this model, experience may trigger or facilitate their development

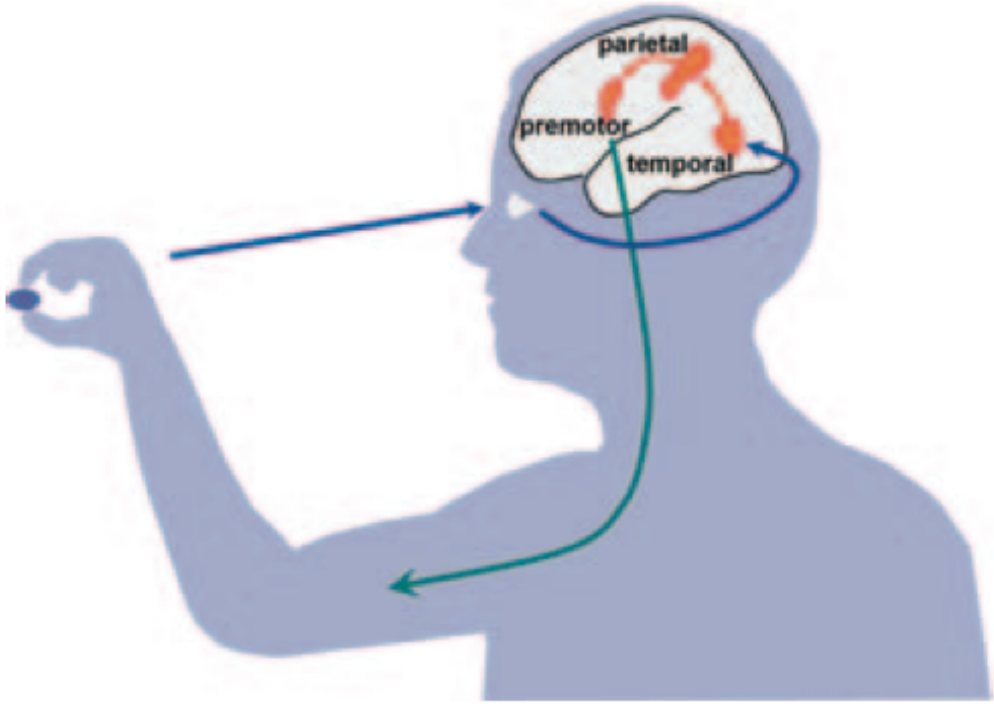
Alternative Explanations

Associative Learning Hypothesis

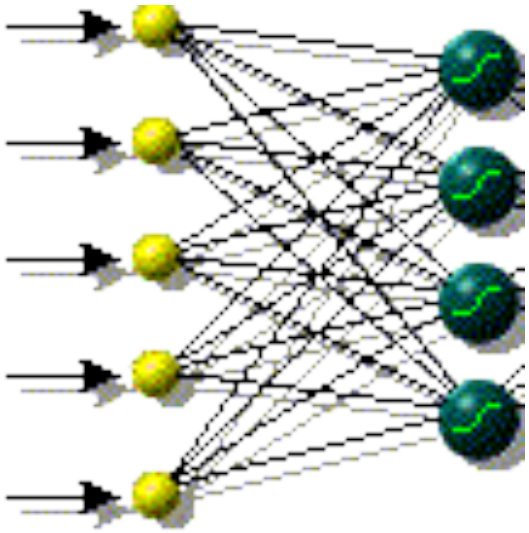
- MNs are the result of associative learning
- Associative learning results from conditioning or the exposure to a relationship between two events
  - Such conditioning is a function of “contiguity,” meaning that the closer two events are in time, the stronger the association
  - It is also a function of “contingency,” that is, one event must reliably predict the other
  - the change in behavior results primarily from the strengthening of connections between event representations. Neurally, this means increasing efficacy of synaptic transmission
  - ‘What fires together wires together’ (Hebbian Learning).

Hebbian Learning

- Activity in the premotor cortex leads to grasping movement. The movement is seen by the individual causing activity in neurons in the occipital and temporal cortex, where it finds neurons that are active because the subject is currently performing the action.



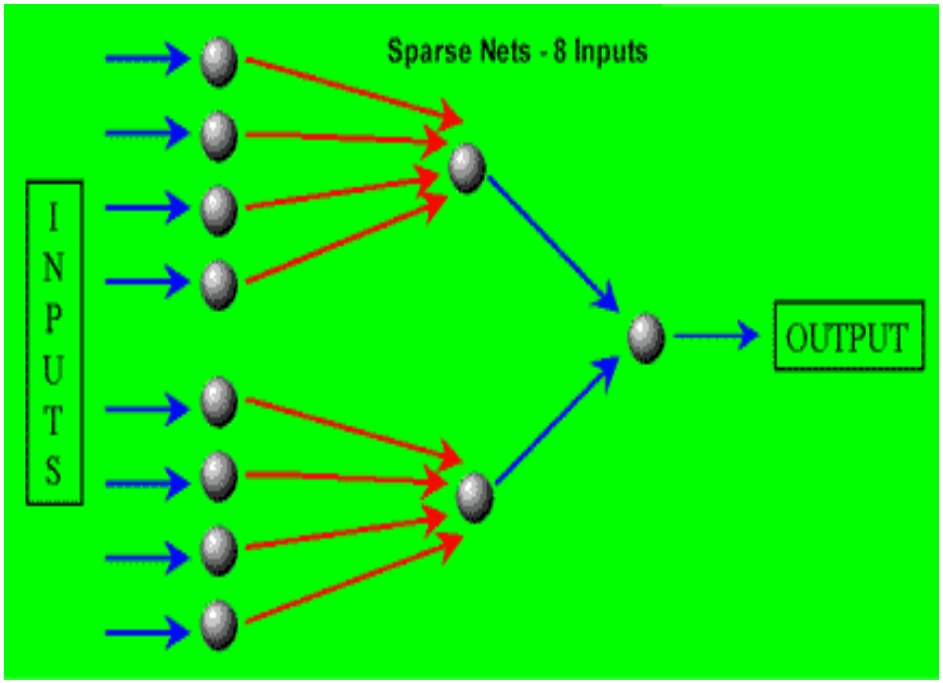
Exhuberancy in Synaptogenesis



Activity-dependent synaptic modification:

- correlated activity
- competition
  - space
  - growth factors
  - targets

Neural Darwinism

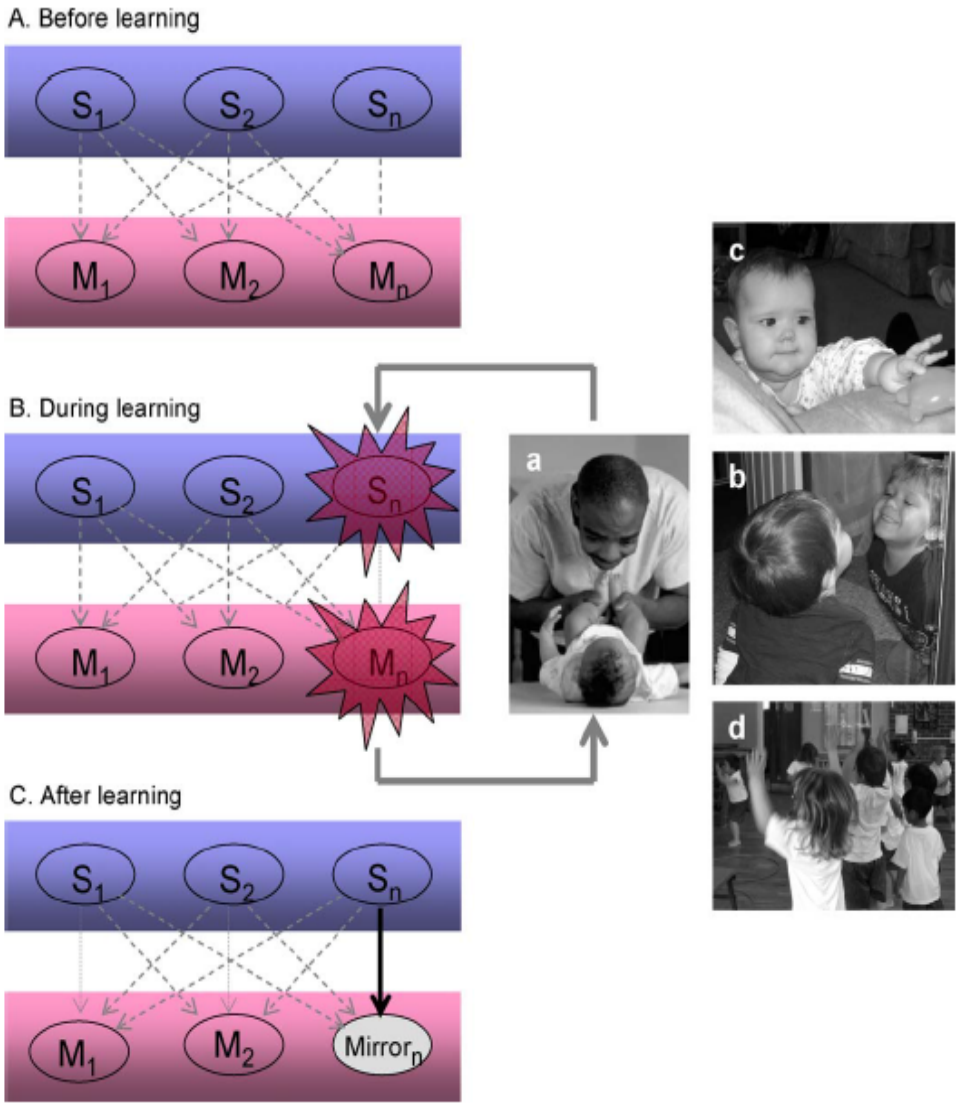


Hebbian Learning Rules
(Adjusting weights at the synapse)

- Synaptic efficacy increases if there is correlated activity in the pre- and post-synapse
- Synaptic efficacy decreases if there is uncorrelated activity in the pre- and post-synapse

Associative Learning Hypothesis

- MNs are forged through sensorimotor experience, that is, correlated experience of observing and executing the same action.



Is This a Nature vs Nurture Dichotomy?

- Heyes argues that it is not
  - Each hypothesis acknowledges genetic and experiential contributions to MN development
  - However, the implications are different, with the associative hypothesis having some advantages over the adaptation hypothesis
    - It provides an empirically testable explanation for the differences between monkeys and humans
    - It explains the existence of mirror neurons in many areas of the brain
    - It is consistent with evidence indicating that MNs contribute to a range of social cognitive functions, but do not play a dominant, specialized role in action understanding
    - It's supported by recent data showing that, even in adults, one can reconfigure the MNS by sensorimotor learning

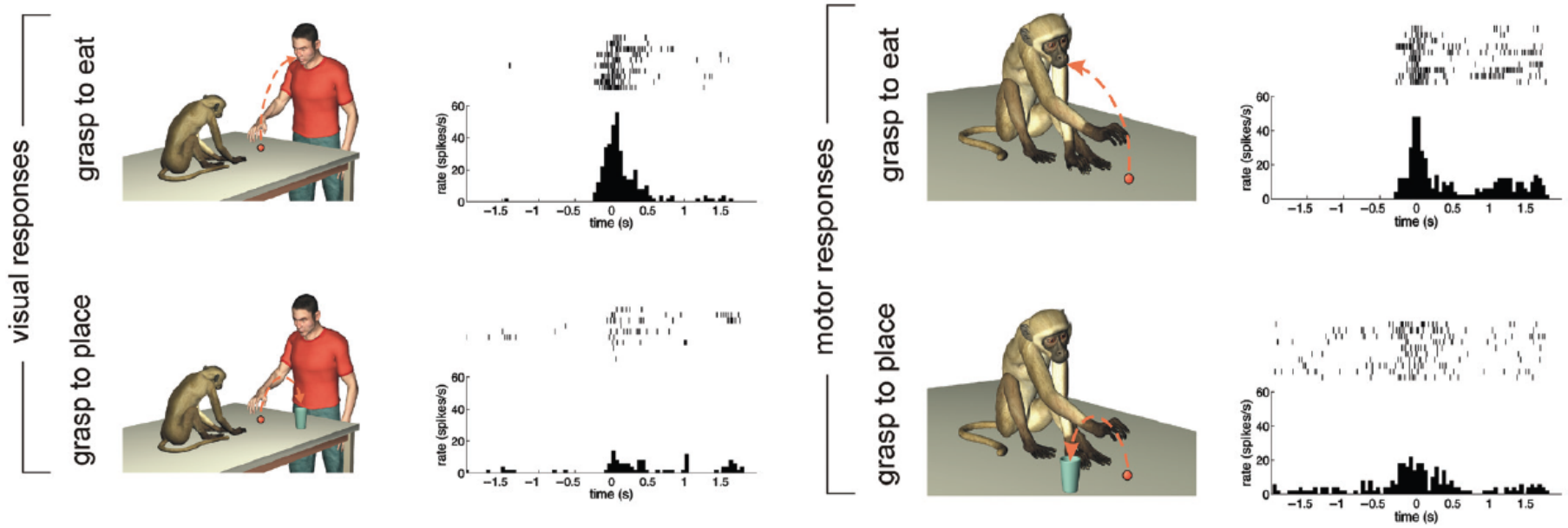
Properties of Mirror Neurons in Monkeys

- Matching property
  - Neurons fire when the monkey observes and performs similar actions.
  - This enables the monkey to understand observed actions by matching them to the monkey's motor plans for the same actions.
  - the matching property of mirror neurons promotes action understanding because it puts the observer in the same causal state as the actor.

The associative hypothesis explains matching property in that whenever a monkey performs a grasping action with visual guidance, the activation of motor neurons (involved in the performance of grasping) and visual neurons (involved in the visual guidance of grasping) is correlated and become mirror neurons, firing not only when grasping is executed, but also when it is observed.

The Role of Context

- Mirror neuron firing is modulated by the context in which an action is observed
  - Fogassi et al., 2005 showed that different populations of parietal mirror neurons fire when a monkey grasps an object that is subsequently eaten and when it grasps an object that is subsequently placed in a container.



The Role of Context (cont)

- Adaptation Hypothesis: the firing of mirror neurons can be modulated by events that occur in the future suggests that the evolutionary function of mirror neurons is to enable an observing animal to infer or predict an actor's intentions.
- Associative Hypothesis
  - As a result of conditional learning, mirror neuron firing can be modulated by events that occur with or before the primary action
  - In the Fogassi study, a container was always presented in trials involving grasping before placing, and never in trials involving grasping before eating. Therefore, the presence or absence of a container could become a conditional cue differentially activating two groups of grasping mirror neurons.

Imitation in Newborns

- The presence of imitation in newborns who have had little opportunity for sensorimotor learning supports the adaptation hypothesis
- But, recent reviews suggest that human neonates reliably match only one action, tongue protrusion; that this effect is transitory; and that it is due, not to imitation, but to a non-specific arousal mechanism.

Effects of Experience

- Ferrari et al., 2005 showed that monkeys who do not initially exhibit mirror neurons to tool use do so after animals receive many opportunities to observe humans using a stick or pliers as a tool, and subsequently to grasp the object themselves
- Calvo-Merino et al., 2006 showed that experts in one type of movement (ballet) are more sensitive to those specific movements than experts in a different type of movement (capoeira)

**** Support an associative learning explanation ****

Effects of Sensorimotor Training Experience

Sensorimotor experience can affect mirror activation in a variety of ways:

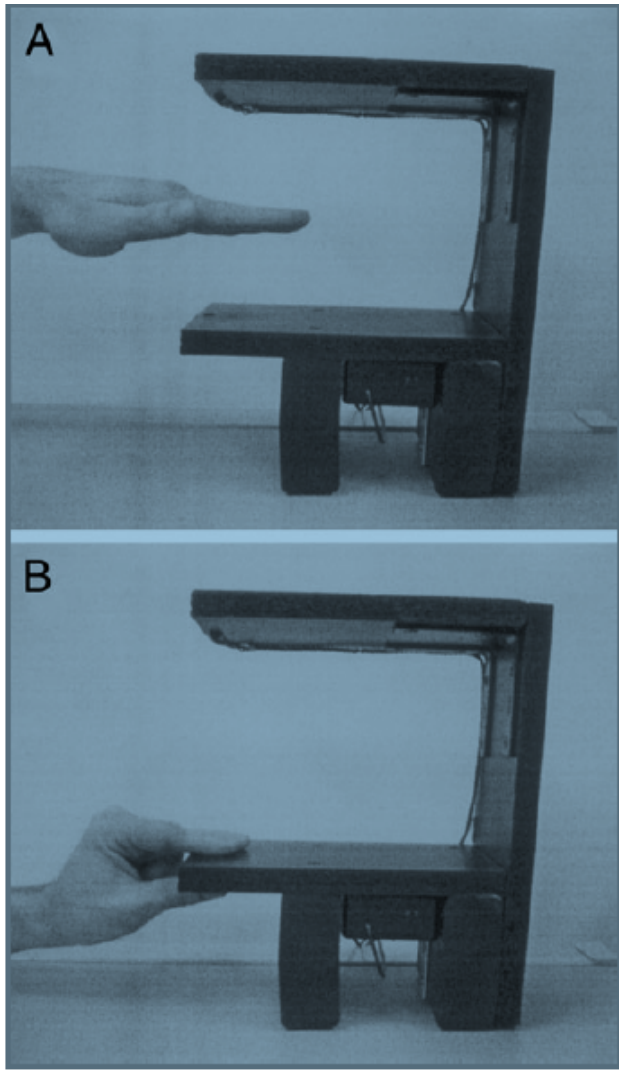
- Enhance (Press et al., 2007)
- Abolish (Heyes et al., 2005)
- Reverse (Catmur et al., 2007 2008)
  - MNS is typically more responsive to hand than foot movements. Watching foot movements while performing hand movements can reverse this relationship
  - Similarly, if you pair the observation of index finger movement with the execution of little finger movement eventually the brain will produce more activity in little finger muscles than in index finger muscles when you observe an index finger (counter-mirror activation).
- Only a brief period of this kind of experience (0.5–2.5 h) induced changes in mirror system properties that lasted for at least 24 h.

Electrophysiological Evidence

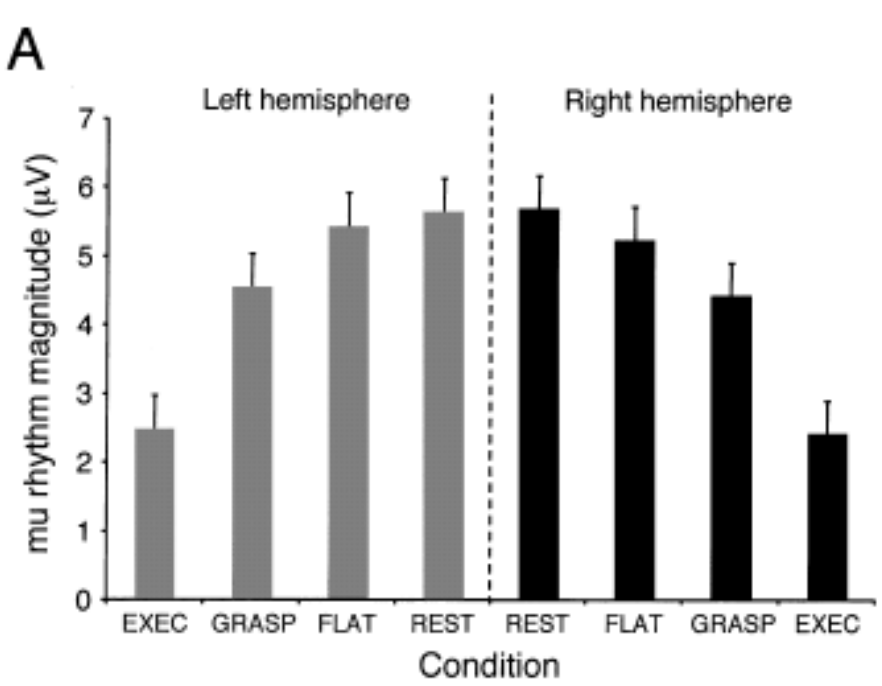
- Fecteau et al. (2004) showed that in a 36-month-old child undergoing intracranial recording for intractable epilepsy, there was a reduction of spectral power in the alpha (7.5–12.5 Hz) band during the execution of hand movements as well as during observation of similar movements compared with a resting condition.
- This frequency band encompassed the mu rhythm, which is thought to reflect sensorimotor processing in the frontoparietal network (Pineda, 2005).

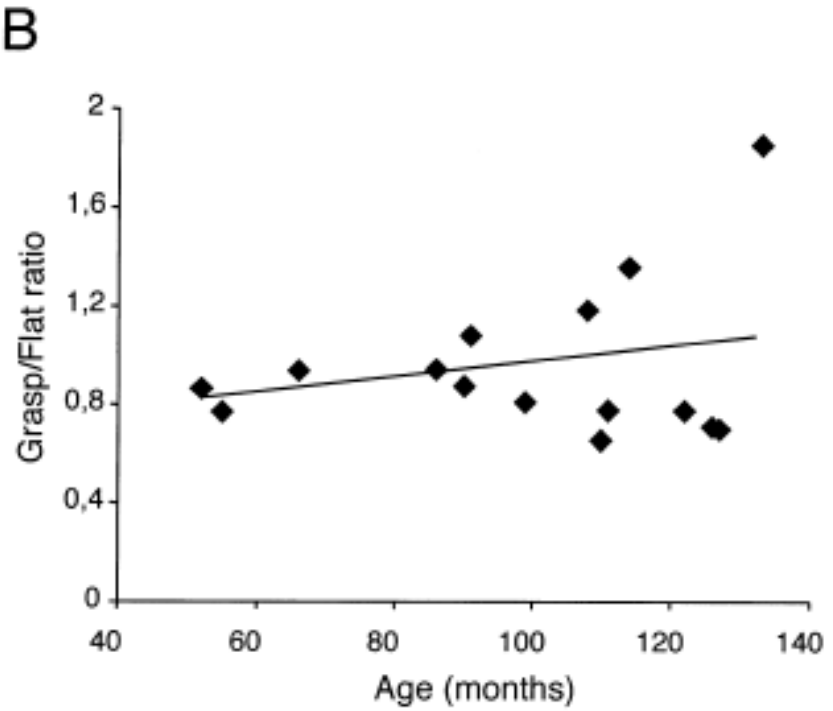
Lepage and Theoret, 2006

- N=18 healthy children (eight males, 10 females) with no history of neurological or psychological problems aged 4-12 yrs watched the experimenter interact with an apparatus.
- Four conditions: rest, flat, grasp, execute



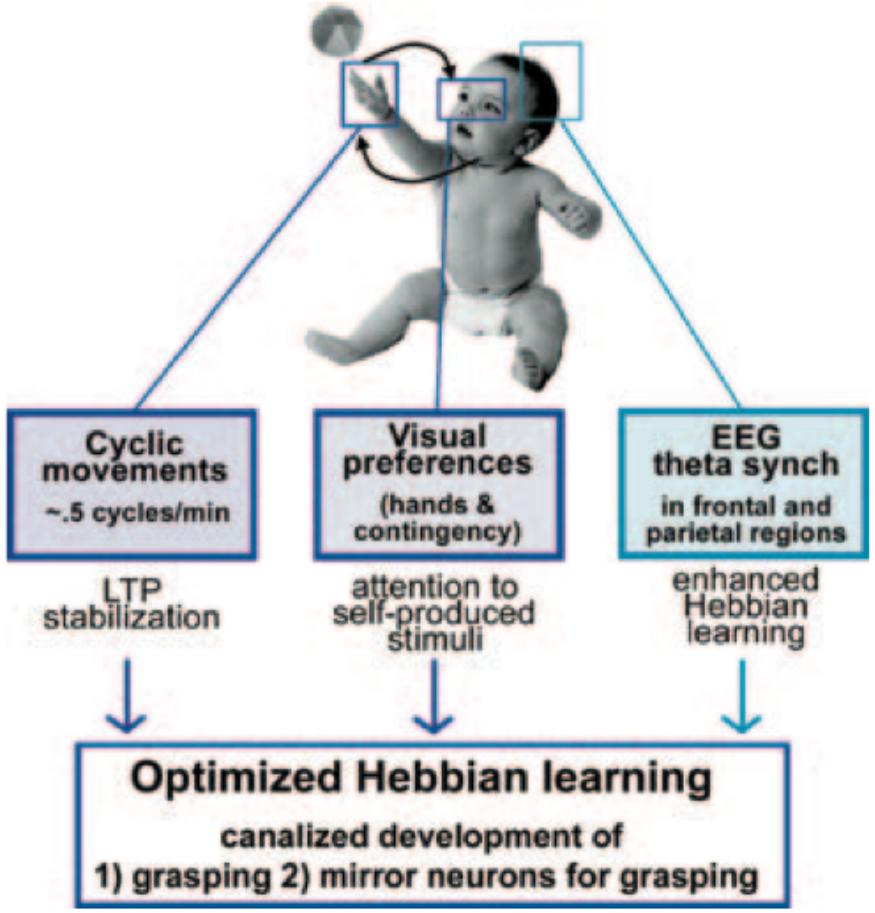
Results


A
Left hemisphere
Right hemisphere
mu rhythm magnitude (μV)
0
1
2
3
4
5
6
7
EXEC
GRASP
FLAT
REST
REST
FLAT
GRASP
EXEC
Condition


B
Grasp/Flat ratio
0
0,4
0,8
1,2
1,6
2
40
60
80
100
120
140
Age (months)

Sources of Sensorimotor Experience

- Human infants like to watch their own hands in motion, which may promote the development of mirror neurons through sensorimotor learning
- Some have proposed that Hebbian learning and genetic pre-programming can be integrated in a broader perspective, by suggesting that the MNS might initially develop through experiential canalization of Hebbian learning



What is Canalization?

- Waddington (1942) and Schmalhausen (1949)
  - A developmental process that is buffered against perturbations. It ensures that important features of the organism emerge reliably, resulting in invariant species-typical development, despite great variation between individuals in environmental conditions and genotypic makeup.

Sources of Sensorimotor Experience (cont)

- One could argue that MNS is, therefore, both an adaptation and a product of associative learning
- However, there is no direct evidence that the tendency of human infants to watch their own hands evolved specifically to promote mirror neuron development.
- It's more likely to be an adaptation for acquiring precise visuomotor control over hand and finger movements

The Mirror Neuron System: A Fresh View (Casile et al., 2011)

- There are really two mirror neuron systems
  - Facial imitative abilities (innate) but subject to modification through social experience.
  - Coordinated development of manual motor skills and action understanding capabilities (learned)
- Sugita (2008) tested the face-processing abilities of macaque monkeys reared with no exposure to face stimuli.
  - deprivation periods of up to two years did not interfere with the recognition and discrimination performance of face stimuli.
- Ferrari and co-workers (2008) reported that the mu rhythm was suppressed in newborn (1-7 days old) monkeys when they observed and imitated facial gestures but not during the observation of nonbiological movements.

Hand Movements

- On the contrary, the development of reaching-grasping movements involves a long period of maturation and requires many levels of sensorimotor integration
- Held and Bauer (1967) dissociated vision and proprioception by preventing newborn macaques from seeing their own arms at birth. When tested at 35 days of age, the subjects exhibited severe impairments in visually guided reaching and grasping
  - correct development of spatial maps of the peri-personal space for goal-directed hand movements entails the observation of own movements.