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PAPER

Programmed to learn? The ontogeny of mirror neurons

Marco Del Giudice,¹ Valeria Manera¹ and Christian Keysers²

1. Center for Cognitive Science, Department of Psychology, University of Turin, Torino, Italy

2. BCN NeuroImaging Center, University of Groningen, Groningen, The Netherlands

Abstract

Mirror neurons are increasingly recognized as a crucial substrate for many developmental processes, including imitation and social learning. Although there has been considerable progress in describing their function and localization in the primate and adult human brain, we still know little about their ontogeny. The idea that mirror neurons result from Hebbian learning while the child observes/hears his/her own actions has received remarkable empirical support in recent years. Here we add a new element to this proposal, by suggesting that the infant's perceptual-motor system is optimized to provide the brain with the correct input for Hebbian learning, thus facilitating the association between the perception of actions and their corresponding motor programs. We review evidence that infants (1) have a marked visual preference for hands, (2) show cyclic movement patterns with a frequency that could be in the optimal range for enhanced Hebbian learning, and (3) show synchronized theta EEG (also known to favour synaptic Hebbian learning) in mirror cortical areas during self-observation of grasping. These conditions, taken together, would allow mirror neurons for manual actions to develop quickly and reliably through experiential canalization. Our hypothesis provides a plausible pathway for the emergence of mirror neurons that integrates learning with genetic pre-programming, suggesting new avenues for research on the link between synaptic processes and behaviour in ontogeny.

Introduction

Human development would be unthinkable without the capacity to learn by observing others' behaviour. 'Mirror neurons', first described in the premotor cortex of macaque monkeys (Gallese, Fadiga, Fogassi & Rizzolatti, 1996; Keysers, Kohler, Umiltà, Nanetti, Fogassi & Gallese, 2003; Kohler, Keysers, Umiltà, Fogassi, Gallese & Rizzolatti, 2002) have the property of responding both while the individual executes an action and while he/she sees or hears another individual performing a similar action. This suggests that these neurons are part of a circuit that translates the actions of other individuals into the language of the observer's own actions, enabling the observer empathically to understand the actions of others while at the same time learning to perform a similar action (e.g. Iacoboni & Dapretto, 2006; Keysers & Gazzola, 2006; Rizzolatti & Craighero, 2004). Clearly, mirror neurons are not the only way in which a viewer can process actions: general visual processing mechanisms can enable humans to view and understand movements that are not within their action repertoire. When an action is, however, within the motor repertoire of an observer because he/she has performed very similar actions or at least actions with a similar goal (Gazzola, Rizzolatti, Wicker & Keysers, 2007a; Gazzola, van der Worp, Mulder, Wicker, Rizzolatti & Keysers, 2007b), mirror neurons could enrich perception of the action considerably, by linking it with the wealth of privileged knowledge deriving from having performed it.

Such privileged knowledge includes the motor program used to perform the action (in particular the way the action unfolds in time), allowing the observer to predict future movements (Umiltà *et al.*, 2001) and potentially replicate the action, and also the somatosensory feelings (Gazzola, Aziz-Zadeh & Keysers, 2006; Gazzola *et al.*, 2007a, 2007b; Keysers *et al.*, 2004) and the emotions associated with that action (for example in the case of facial expressions: Jabbi, Swart & Keysers, 2007; Wicker Keysers, Plailly, Royet, Gallese & Rizzolatti, 2003).

There has been considerable progress in describing the location and function of the mirror neuron system (MNS) in the primate and human brain (Buccino, Binkofski & Riggio, 2004; Gallese, Fadiga, Fogassi & Rizzolatti, 1996; Gazzola *et al.*, 2006; Grafton, Arbib, Fadiga & Rizzolatti, 1996; Iacoboni, Molnar-Szakacs, Gallese, Buccino, Mazziotta & Rizzolatti, 2005; Keysers *et al.*, 2003; Keysers & Gazzola, 2006; Kohler *et al.*, 2002; Rizzolatti & Craighero, 2004; Rizzolatti, Fadiga, Gallese & Fogassi, 1996; Umiltà *et al.*, 2001). If mirror neurons are important for the social development of children, understanding how mirror neurons themselves develop is an important question for developmental psychology and neuroscience. However, we still know surprisingly little about their ontogeny (Lepage & Théoret, 2007; Kilner & Blakemore, 2007; but see also Shimada & Hiraki, 2006). Are mirror neurons (MNs) the result of learning processes, or do they acquire their function by genetic pre-wiring? Proponents of the former (Arbib, 2004; Brass & Heyes, 2005; Keysers

Address for correspondence: Marco Del Giudice, Center for Cognitive Science, Department of Psychology, University of Turin, 10123 Torino, Italy; e-mail: marco.delgiudice@unito.it

& Perrett, 2004) maintain that, given the existing anatomical connections between temporal, parietal and premotor areas, some neurons will acquire 'mirror' properties following a simple neural learning phenomenon: Hebbian synaptic potentiation, sometimes paraphrased as 'what fires together wires together', can link motor neurons involved in producing an action with visual/auditory neurons responding to the sight/sound of the action itself. A remarkable body of recent evidence seems to support this learning-based account (see below).

Many researchers, however, remain skeptical (Bertenthal & Longo, 2007; Hurford, 2004; Meltzoff, 2005; Meltzoff & Decety, 2003; Rizzolatti, Fadiga, Fogassi & Gallese, 2002), or explicitly favour explanations involving some amount of genetic predisposition at the neuron level (Lepage & Théoret, 2007; Piattelli-Palmarini & Bever, 2005). From the evolutionary point of view, it is indeed reasonable to expect that an ability as crucial for survival as action recognition and learning through observation would become pre-programmed ('innate') to some degree during phylogenetic history; however, the critical issue of *how* MNs could be pre-programmed to perform their task is rather unclear. Thus, the controversy remains unresolved, and our understanding of MNS ontogeny is still partial and unsatisfactory. Here we propose 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* (Gottlieb, 1991a) of *Hebbian learning* (Keyesers & Perrett, 2004). We argue that this hypothesis, while admittedly speculative, has three distinct advantages: it goes beyond simple nature–nurture dichotomies and is consistent with current evolutionary biology; it helps to make sense of some otherwise puzzling developmental phenomena; and it suggests interesting new questions for empirical research. The paper is organized as follows: we will begin by describing the concept of canalization and the Hebbian learning hypothesis; then we will present our ontogenetic model; and finally we will review the empirical evidence in support of our position.

Experiential canalization

Imagine a young bird that has to recognize what birds of its own species sound like in order to follow its mother's calls. How can natural selection accomplish this crucial task? In the simplest innatist account, the bird's brain could be hardwired during foetal development to recognize the sound of birds of the same species. This would ensure a quick response (no learning time is required) and robustness against spurious associations; however, the process would require precise stimulus matching, substantial genetic specification, and could end up being very sensitive to minor perturbations of neuronal wiring (owing to genetic or developmental factors). In the simplest learning account, the bird could simply associate what it hears and sees until it develops an appropriate representation of its mother's sound. This would allow

for greater flexibility; however, there may be prices to pay, in terms of slowness resulting from trial-and-error learning and susceptibility to spurious associations (for example, the bird hears calls of another species). Although some ontogenetic processes might have been selected to unfold in such narrowly specified ways, there is another possibility, one that allows for both robustness and flexibility: development guided by *experiential canalization*.

Canalization, first conceptualized by Waddington (1942) and Schmalhausen (1949), means that a developmental process is buffered against perturbations: canalization 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 (see Flatt, 2005; Niven, 2004). Development results from interactions between genes and environment, and, crucially, both genes *and* environment can act as sources of invariance and stability; canalization is the result of predictable interactions between genetic mechanisms and reliable features of the environment (West-Eberhard, 2003). Often, the organism's sensory experience plays an essential role in directing ontogeny, leading to experiential canalization (Gottlieb, 1991a). A classic example is the development of ducklings' preference for species-specific auditory features of maternal calls. Ducklings raised in incubators, without previous experience of maternal stimulation, nevertheless spontaneously exhibit the 'correct' preference for their own species' maternal calls. This might prompt some to attribute such preference to some form of pre-wiring in the auditory brain system, with some innate encoding of species-typical acoustic patterns. However, the key factor appears to be the early exposure to *self-produced vocalizations*, which themselves contain the correct acoustic features: if ducklings are experimentally prevented from hearing their own vocalizations, they subsequently fail to exhibit selective responses to maternal calls (Gottlieb, 1991b). Far from denying the importance of genetic effects, experiential canalization emphasizes the need to dissect the epigenetic pathway to find out *how* genes, environment and experience interact to shape development. In this particular case, genetic factors indirectly influence brain development in at least three ways: (1) by affecting the anatomy and physiology of the duckling's vocal apparatus; (2) by affecting the duckling's tendency to produce early vocalizations; and (3) by predisposing its auditory system to learn from vocalizations, just at the right time.

The Hebbian mirror system

The idea of Hebbian learning in the mirror system has been proposed to show that the MNS *could* develop without the need for genetic pre-wiring (Keyesers & Perrett, 2004), without necessarily denying the possibility of genetic predetermination. In a nutshell, this model makes three assumptions: (1) anatomical connections exist between the temporal, parietal and premotor areas involved in the mature mirror system; (2) these connections are

actions as goal-directed significantly more often than did controls. The reverse was not true, however: repeated observation of other-produced grasping did not facilitate infants' grasping execution. Taken together, these results are consistent with the idea that grasping execution and recognition are coupled and causally related, as would be expected if repeated self-observation was needed for developing a MNS and successfully recognizing other individuals' grasping. An interesting topic for future research would be to investigate whether infants who cannot perceive themselves grasping objects (for example infants born with motor problems, such as brachial plexus injuries) undergo a delay in their ability to recognize grasping actions as goal-directed.

Further support for the learning account comes from the field of artificial intelligence, where neural network simulations have repeatedly shown that mirror properties can emerge from recurrent inputs, both in the visual (Metta, Sandini, Natale, Craighero & Fadiga, 2006; Oztop & Arbib, 2002; Oztop, Bradley & Arbib, 2004) and in the auditory (Westermann & Miranda, 2003) domain. Other (indirect) support comes from evidence of MNS plasticity in the adult brain in the acquisition of new motor skills (Calvo-Merino, Glaser, Grèzes, Passingham & Haggard, 2005; Calvo-Merino, Grèzes, Glaser, Passingham & Haggard, 2006; Catmur *et al.*, 2007; Cross, Hamilton & Grafton, 2006; Haslinger *et al.*, 2005; Lahav *et al.*, 2007).

Developmental canalization of the Hebbian mirror system

Combining the concept of experiential canalization with that of Hebbian learning raises the intriguing possibility that evolution may not have taken the direct route of pre-wiring neurons with perceptual preference for a particular action with premotor neurons coding for the same action. Actually, this form of predisposition implies the possession of innate representations of others' actions, which may pose a formidable obstacle given the complexity of human (and primate) manipulative ability. Instead, natural selection could have obtained the same result indirectly, by adjusting the parameters of infant behaviour so as to provide optimized conditions for Hebbian training of visuomotor neural associations, which would result in canalized development of the MNS, at least for some basic actions such as hitting, pushing and grasping. Here we will concentrate on hand actions, but towards the end of the paper we will show how experiential canalization of a different nature could help to explain how a mirror system can develop for facial expressions. For hand actions, we propose that evolved mechanisms: (1) selectively bias infants towards observation of their own actions; and (2) optimize the parameters of self-produced motor patterns so as to maximize correct Hebbian learning at the synaptic level. This interplay of perceptual and motor features would make for highly canalized development of the MNS, even without genetic pre-wiring of the neurons themselves

(Figure 2). Action recognition is a sophisticated form of species-typical perception; experiential canalization increases the efficiency of trial-and-error processes, resulting in fast and reliable learning of crucial sensory patterns. Much in the same way as ducklings self-produce the auditory stimuli that will allow them to recognize their mother's calls, human infants self-produce the visuomotor stimuli that will allow them to attribute immediate meaning to others' actions in the world. Of course, visuomotor learning is not exclusively (or even primarily) targeted at MNS development, but is needed for performing the actions themselves; in fact, we do not think that it is possible to separate the emergence of mirror properties in the visuomotor system from the process of learning to grasp, hit, push and so on (see Figure 2). The canalization of Hebbian learning that we propose to facilitate development of the MNS would therefore be stabilized by evolutionary pressures to develop a well-coordinated visuomotor system.

Although it is of course difficult to devise a straightforward test of this evolutionary/developmental hypothesis, we can examine if infants actively look at their own actions, and if their self-produced motor patterns seem to provide for optimized synaptic learning. We will use grasping as

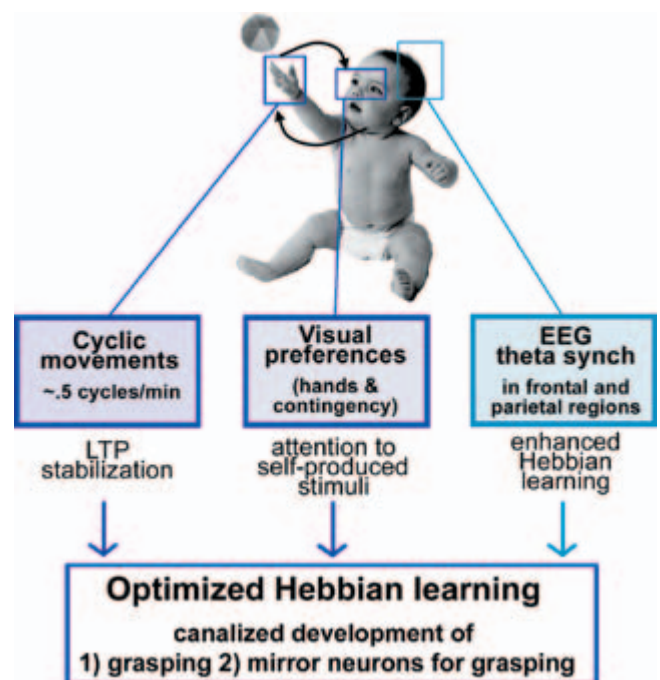


Figure 2 The development of mirror neurons for grasping in our ontogenetic model. Infants' motor and perceptual characteristics lead to canalized Hebbian learning via observation of self-produced actions. Visual preference for hands, together with a preference for perfect action-perception contingency, directs infants' attention towards salient stimuli. Cyclic patterns of spontaneous movement provide optimal timing for stabilizing long-term potentiation (LTP) at the synaptic level; EEG synchronization at theta frequency (linked to attention) further enhances Hebbian learning, probably by coordinating neuronal firing in the proper time window.

our core example, because it is well studied from the physiological and developmental point of view. We will show that infants indeed selectively attend to their own actions early in infancy, and then (only gradually) shift their focus of attention to the hands of others. We will then try to identify what behavioural and neurophysiological parameters would be optimal to promote efficient Hebbian learning, and finally argue that the regularities of infants' self-produced motor patterns could have evolved to match those optimal parameters.

An ontogenetic model of the Hebbian mirror system

Infants' visual preferences

Infants' early preference for looking at faces is well known (e.g. Fantz, 1963; Johnson & Morton, 1991; Macchi Cassia, Turati & Simion, 2004; Turati, Macchi Cassia, Simion & Leo, 2006). It is less well known that infants have a marked visual preference for *hands* as well. Research findings show that hands are extremely salient stimuli, starting from the first days of life: in what is still the most thorough observational study of infants' reaching, White, Castle & Held (1964) showed that 2–3 month olds spend most of their waking time looking at their own hands. More recently, a notable set of experiments proved this process to be purposeful and intentional: newborns actively try to control arm movements in order to keep their hands visible, even if effort is required, and they also move their hands significantly more when they can watch them, showing a clear preference for hands in motion (van der Meer, 1997; van der Meer, van der Weel & Lee, 1995; von Hofsten, 2004). Infants' visual attention is also captured by their own reaching and grasping attempts; as early as 2 months, they begin to perform so-called *alternating glances* (i.e. the infant raises a hand near a reachable object, then starts looking back and forth between hand and object; White *et al.*, 1964).

Infants' preference for hands becomes especially relevant to our model when coupled with their selective attention towards *contingent* stimuli. The ability to detect spatial and temporal contingency is present shortly after birth (Lemelin, Tarabulsky & Provost, 2002; Tarabulsky, Tessier & Kappas, 1996). Until 3 months of age, infants show a preference for perfectly contingent events; that is, for events whose sensory timing perfectly matches the infant's proprioceptive sensation (Gergely & Watson, 1999). Apart from experimental settings, perfect contingencies usually arise from self-produced actions; this preference is thus likely to orient younger infants towards self-exploration. At about 3–4 months a developmental shift occurs, with infants showing preference for spatially and temporally non-contingent movements, which usually are not self-produced (Bahrick & Watson, 1985; Rochat, 1998; Rochat & Striano, 2000; Schmuckler, 1996; Schmuckler & Fairhall, 2001). This shift in preference has two

consequences. First, it directs the infant's attention to actions that his developing brain does not yet fully predict. Second, it focuses the infant's attention on the hand-actions of other people, potentially promoting learning by observation. Indeed, after the first semester, visual preference for an adult's hands can overcome even that for an adult's face, particularly when the hands are moving and manipulating objects (Amano & Kezuka, 1994; Amano, Kezuka & Yamamoto, 2004). In summary, research on early visuomotor development suggests that, until 3 months, infants are particularly attracted by self-produced movements, especially by their reaching and grasping attempts. These perceptual preferences ensure that infants have access to a large amount of input for Hebbian learning in the MNS.

What are the optimal conditions for Hebbian learning?

Unfortunately, most neuroscience research on the process of synaptic long-term potentiation (LTP), which is thought to underpin Hebbian learning at the neuron level, has focused exclusively on the millisecond timescale (Bi & Poo, 2001; Berninger & Bi, 2002; Bi & Rubin, 2005; Dan & Poo, 2006). As a result, we know relatively little about the 'macro-temporal' conditions for Hebbian learning (i.e. in the second-to-minute scale) that can be optimized in actual behaviour. Three factors nevertheless appear particularly important in promoting and sustaining LTP: (1) cyclic stimulus presentation; (2) optimally spaced repetition of stimuli (i.e. optimal periodicity); and (3) EEG synchronization at theta/gamma frequencies. In vivo, a single episode of synchronized pre- and post-synaptic activity leads to an LTP that fades quickly. Repeating the episode after a certain interval can prevent this spontaneous LTP reversal. In the *Xenopus* frog's retina, long-term effects of LTP are maximized if trains of stimuli are applied every 5 minutes, whereas LTP consolidation approaches zero for intervals longer than 10 minutes, with a quadratic relationship existing between time interval and stabilization (Zhou & Poo, 2004; Zhou, Tao & Poo, 2003; see Figure 3b). In addition, local EEG rhythms at theta (3.5–7 Hz) and gamma (30–70 Hz) frequencies also facilitate Hebbian learning, possibly via synchronization of neuronal firing in the LTP time window (Griffin, Asaka, Darling & Berry, 2004; Kahana, Seelig & Madsen, 2001; Miltner, Braun, Arnold, Witte & Taub, 1999; Paulsen & Sejnowsky, 2000; Seager, Johnson, Chabot, Asaka & Berry, 2002).

The cyclic organization of infant motor patterns: optimized for Hebbian learning?

Spontaneous motor activity in foetuses and infants is indeed cyclic. Activity and rest phases alternate with an average low-frequency period of about 2 minutes (0.5 cycles/min) (Robertson, 1982, 1985, 1987, 1988, 1990, 1993a, 1993b; Robertson, Bacher & Huntington, 2001; Robertson & Dieker, 1986, 2003; Robertson, Dierker,

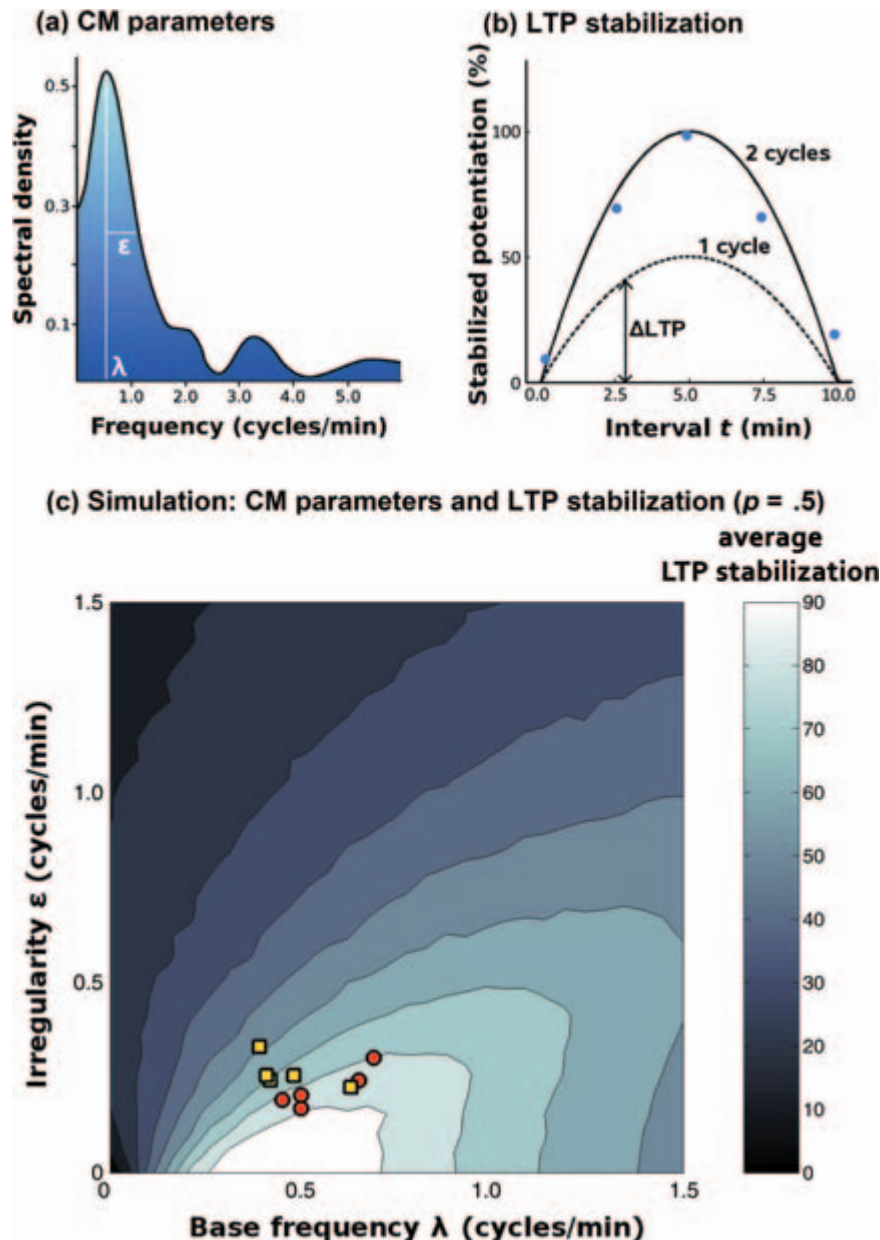


Figure 3 A simple mathematical model of synaptic long-term potentiation (LTP) following cyclic learning. (a) Typical spectral plot showing cyclicity in infant movements (CM). The cycle's base frequency λ is about .5 cycles/min (cycle duration: 2 min), and irregularity is represented by the standard deviation ϵ (assuming normal distribution around λ). (b) Quadratic LTP stabilization function modelled on the empirical data reported by Zhou et al. (2003). Dotted line: stabilization after one cycle. Solid line: stabilization after two cycles. ΔLTP is the increase in stabilized potentiation after one cycle of duration t . Blue circles show the average LTP levels measured by Zhou et al. (2003) after two learning cycles. (c) Contour plot of simulation results with p set to .5, showing the relationship between cycle period (λ), cycle irregularity (ϵ) and performance in LTP stabilization. Lighter colours represent a higher average increase in stabilization over 30,000 simulated cycles (note: values are rescaled so that 100 corresponds to the local maximum). The pattern to be learned (i.e. a specific movement, such as precision grasping) occurs every cycle with probability $p = .5$. The optimal frequency λ increases for increasing values of ϵ and for decreasing values of p (see text). Superimposed symbols show the average values of λ and ϵ in published studies of human foetuses (squares) and newborns/infants (circles); each symbol corresponds to one study. See Appendix for details and references.

Sorokin & Rosen, 1982). In addition, spontaneous movements embed irregular fluctuations, seemingly characterized by non-random chaotic dynamics (Robertson, 1993a, 1993b; Robertson *et al.*, 2001). Spontaneous motor activity usually involves the entire body (Almli, Ball & Wheeler, 2001; Groome *et al.*, 1999), including arms and hands,

which are often moved repeatedly in short bouts of activity (Adolph & Berger, 2005; Piaget, 1962). Cyclic movements (CM) with similar characteristics have also been reported in rat and sheep foetuses (MacLennan, Smotherman & Robertson, 1998; Robertson & Bacher, 1995; Robertson *et al.*, 1996; Smotherman, Robinson &

Robertson, 1988; Suzue & Shinoda, 1999), probably representing an ubiquitous feature of mammalian motor development.² In humans, they persist after birth until at least 4–5 months of age (Groome *et al.*, 1999; Robertson, 1987, 1990, 1993a). Remarkably, some kinetic features of spontaneous movements tend to be stable from foetuses to 5-month-old infants, despite changes in physical parameters such as arm weight and length (von Hofsten & Rönnqvist, 1993). The function of CM remains controversial, and various hypotheses have been put forth. CM could be functional to foetal neuromuscular and motor development in early phases, and may later help to regulate an infant's interaction with his/her physical and social environment by alternating phases of activity and externally directed attention (Bacher & Robertson, 2001; Robertson, 1985, 1987, 1989; Robertson *et al.*, 2001).

In the context of our hypothesis, a key function of CM (and, especially, of their persistence in the first 4–5 months of human life) may be the optimization of Hebbian learning in the brain via enhancement of LTP consolidation. As described above, optimally spaced learning cycles seem effective in preventing LTP reversal, with the data available so far suggesting an optimal frequency of about .2 cycles/min. Of course, the discrepancy between the 'synaptic optimum' of .2 cycles/min and the behavioural rhythm of about .5 cycles/min may depend on fundamental differences in the neural cells of *Xenopus* frogs versus those of mammals and humans, or simply on our hypothesis being wrong. However, other less obvious possibilities exist. First, CM cycles are quite irregular (see above), whereas the stimuli employed in the *Xenopus* experiments were extremely regular. Second, foetuses and infants do not repeat exactly the same movements from cycle to cycle, leading to effectively longer inter-stimulus intervals; in other words, the probability of performing a given movement pattern (i.e. of presenting the synapse with the 'correct' input) during a given movement cycle is less than one. Both of these factors, absent from laboratory experiments on LTP but affecting infants in ecological conditions, can push the actual optimal frequency higher than would be expected on the basis of synaptic properties alone.

To explore the impact of these factors, we developed a simple mathematical model of cyclic Hebbian learning, based on the LTP consolidation function measured by Zhou *et al.* (2003). By computer simulations (see Appendix for details) we obtained the expected value of LTP consolidation as a function of three parameters: the frequency (λ) and irregularity (ϵ) of CM and the probability (p) of performing the movement pattern in a given cycle (behavioural variability). Our aim was to explore whether

the optimal base frequency varied depending on irregularity and variability, and to investigate the strength of these effects (Figure 3).

Pattern repetition probability (p) obviously affects the model's behaviour: when p is set to 1, the optimal frequency λ is .2 cycles/min (the synaptic optimum). As p decreases, however, the optimal λ increases; in the absence of irregularity, the optimal frequency is just $\lambda^* = .2/p$, and for $p = .4$, it is $\lambda^* = .5$. Although at present no data exist on the probability of motor pattern repetition in foetuses and infants, it seems reasonable to suggest that it should lie in an intermediate range, especially if the infant's motor repertoire is still relatively small. Although this is clearly an open empirical question, our model shows that a behavioural cycle of ~.5 cycles/min can be consistent with a synaptic optimum of .2 cycles/min, provided that infants do not always repeat the same actions from cycle to cycle. In Figure 3(c), we show the model's output when p is set to .5. The degree of irregularity (ϵ) also affects the optimal base frequency: with increasing ϵ , the optimal λ increases, although the effect of ϵ is less dramatic than that of p (and might depend on the exact shape of CM frequency peaks; see Appendix for discussion). As can be seen in Figure 3(c), the empirical data from newborns and infants seem consistent with this prediction, whereas those from foetuses do not appear to follow the same pattern. As mentioned above, irregularity is a robust feature of CM, and is likely to have some intrinsic benefits of its own (for example preventing habituation or generating novel motor patterns), which have not been taken into account in our simplified model. Such irregularity is expected to result in a CM frequency higher than the synaptic optimum.

EEG synchronization during grasping

EEG activation during infants' spontaneous activity is poorly investigated, but infants aged 2–11 months, when reaching and handling objects, show increased theta synchronization (especially in the 4.0–5.8 Hz band) in the parietal and frontal lobes, which are critical for the mirror system (Futagi, Ishihara, Tsuda, Suzuki & Goto, 1998). Frontal theta rhythms (especially 4.4–5.6 Hz), declining from 8 to 11 months, were also observed in the anticipatory phase of a peekaboo game (Orehova, Stroganova & Posikera, 1999; Stroganova, Orehova & Posikera, 1998), which requires the prediction of another individual's behaviour, and could thus be linked to mirror activation. Theta rhythms are often studied focusing on their causes (for example attention, movement control) but, because they affect synaptic learning, their consequences on neural processes should be considered as well.

EEG patterns may also increase our understanding of the development of the MNS by allowing us to indirectly quantify the activity of the infants' mirror systems using mu-suppression. At rest, the premotor/motor cortex appears to generate synchronized activity in the mu-band (8–13, 15–25 Hz); if a subject engages in motor activity,

² Interestingly, a frequency of ~.5 cycles/min was also observed in the spontaneous firing of retinal ganglion cells in ferret foetuses (Shatz, 1996); such endogenous firing patterns are required in mammals for proper neural connection before birth. The widespread time invariance of self-generated rhythms in early development (see Corner, van Pelt, Wolters, Baker & Nuytinck, 2002 for an extensive review) might indeed reveal a deep connection with learning processes at the synaptic level.

this mu-rhythm is suppressed. Interestingly, the same mu-rhythm is also suppressed when the actions of other individuals are being observed (Oberman, McCleery, Ramachandran & Pineda, 2007; Pineda, 2005). Following this principle, the MNS for grasping seems fully developed at 40 months of age (Lepage & Théoret, 2006). Measurements in the age range from 0 to 8 months would be critical to investigate the early development of the mirror system, but changes in the frequency of EEG rhythms throughout the first months of life (Marshall, Bar-Haim & Fox, 2002) render these experiments difficult.

Future research directions

In this section, we describe some empirical tests that could be used to assess the validity of our hypothesis. We also highlight the implications of our proposal for future research: looking at early neural development as an experientially canalized process requires the collection of new types of evidence, both on the structure of early behaviour and on the properties of the neural networks involved.

Properties of infant cyclic movements

We hypothesized that the frequency of spontaneous CM might be close to optimal for enhanced Hebbian learning at the synaptic level. Our simple mathematical model shows that the optimal cyclicality of behaviour need not be equal to the synaptic optimum; in particular, both variability in spontaneously produced movements (which we modelled by pattern repetition probability) and cycle irregularity tend to favour higher cycle frequencies. This model could now be tested by new studies of infant CM, by assessing behaviour variability together with cycle frequency and irregularity.

Some features of our model may also help to shed light on the nature of individual differences in spontaneous motor activity. CM frequency shows a fair amount of inter-individual variation, which led Robertson (1989) to suggest that the exact frequency of CM may not be critical to their function. However, our model predicts that the optimal frequency for a given individual should depend on other parameters, such as cycle irregularity and behavioural variability. If the model were correct, individual differences in CM frequency may relate to one or more of the following: (1) individual differences in behavioural variability; (2) individual differences in cycle irregularity; or even (3) differences on the synaptic side (i.e. in the time function of LTP consolidation). Variation in the LTP consolidation function could be a result, for example, of the relative density of NR2A versus NR2B glutamate NMDA receptors, which has been found to change during development (see Paulsen & Sejnowski, 2000; Quinlan, Philpot, Haganir & Bear, 1999). The model also predicts that infants showing less than optimal combinations of CM parameters should,

all else being equal, exhibit some delay in the acquisition of action recognition and MNS functionality, which could be measured for instance using mu-suppression paradigms.

Macrotemporal conditions for Hebbian learning

We think that much could be gained by investigating the macrotemporal (i.e. minutes to hours) conditions of LTP consolidation. On one side, macrotemporal timescales can be linked more readily to actual behaviour; on the other, following the fate of LTP over longer time intervals will help in gaining an understanding of the complexity of its regulatory mechanisms. We also need data on different species, at various developmental stages; although Zhou *et al.*'s (2003) data are immensely valuable, it is quite possible that results from developing *Xenopus* do not generalize to other species. It is also possible that they do (as we provisionally assumed here), which would be an important result in itself. At the moment, our ignorance of how the details of LTP vary in different organisms prevents the development of more formal models of the Hebbian processes involved in early learning, and limits the generalizability of research findings in this area.

Ontogenetic shifts in preference for contingency

We argued that the preference for perfect contingency in early infancy may be functional to the reliable acquisition of Hebbian association in the developing brain. This leads to a novel prediction: ontogenetically, the shift from perfect to imperfect contingency preference should *follow* the acquisition of basic MNS functionality. Empirically, longitudinal studies over the first 9 months of life could relate individual differences in the timing of shifts in contingency preference to individual differences in the development of action recognition. It may also be that contingency preferences for different kinds of actions (for example hand actions versus facial expressions) shift at different rates, following intra-individual differences in the acquisition of Hebbian associations.

Facial expressions

Self-observation is a clear source of Hebbian learning for actions we can directly perceive. Interestingly, it is also the case that the sight of some facial expressions activates the premotor cortex, which is involved in producing similar expressions (Carr, Iacoboni, Dubeau, Mazziotta & Lenzi, 2003; Ferrari, Gallese, Rizzolatti & Fogassi, 2003; van der Gaag, Minderaa & Keyers, 2007), and the anterior insula, which is involved in experiencing the correspondent emotions (Jabbi *et al.*, 2007; Wicker *et al.*, 2003), thus suggesting the existence of a mirror system for emotions (Gallese, Keyers & Rizzolatti, 2004; Iacoboni & Dapretto, 2006; Keyers & Gazzola, 2006). But how can the brain learn that a particular facial expression corresponds to a particular

motor program and emotional state? The concept of self-observation is unlikely to explain this phenomenon, because we do not usually see our own facial expressions. The finding that neonates imitate certain facial displays (Meltzoff & Borton, 1979; Meltzoff & Moore, 1977) has led to the idea that a mirror system for facial expressions might be inborn, but this interpretation has been criticized, because very few actions (for example tongue protrusion) seem to be reliably imitated (Anisfeld, 1991, 1996, 2001). Recently, an alternative proposal was advanced that maintained that the social world holds up a biological mirror to infants' facial expressions (Heyes, 2001; Keysers & Gazzola, 2006; Keysers & Perrett, 2004). The emotional expressions of the baby often induce adults around him/her to produce similar expressions, which in turn provide the infant with a visual input that matches his motor output and enables Hebbian learning. The concept of experiential canalization might be essential in two ways for this account. First, the tendency of adults to imitate and exaggerate the facial expressions of the baby could be seen as an adaptation that ensures that the baby receives the correct input for Hebbian learning. Second, the infant's attraction for sensory input contingent with his/her motor output (Lemelin *et al.*, 2002; Tarabulsy *et al.*, 1996) could be seen as an adaptation that directs his/her attention towards facial expressions that are reactions to his/her own. Together, these two factors could canalize the Hebbian association between the vision and experience of emotions.

Future research could test this hypothesis by examining quantitatively whether parents do systematically imitate the facial expressions of their children, and whether differences in such imitation result in differences in the children's mirror system for facial expressions at a later stage in development. A testable prediction of this account is that the structure of a co-occurrence matrix between a child's and parent's facial expressions should affect the structure of the facial mirror system. That is to say that if a child's smile is systematically co-occurring with an adult's smile, but a child's distress equally with a parent's anger and distress, one would expect activity in the mirror system and measures of facial mimicry and emotional contagion to associate happiness with happiness but distress with both anger and distress. Another line of evidence could come from the study of the activity of the MNS for facial expression in infants with fewer opportunities to see their parents imitate them (for example, non-blind infants with blind parents). If the social mirror hypothesis were correct, we could expect that infants whose parents do not consistently imitate their facial expressions would show weaker responses in their own motor system to the sight of facial expressions with respect to normal infants.

Finally, further empirical research would be needed to address the question of how neonatal imitation of facial gestures such as tongue protrusion (which start decreasing after the second month of life, virtually disappearing around the fifth month; Abravanel & Sigafos, 1984; Bower,

1976; Fontaine, 1984; Maratos, 1982) relates to the more mature forms of facial imitation observed in children from the end of their first year of life (Myowa-Yamakoshi, 2001). Myowa-Yamakoshi, Tomonaga, Tanaka & Matsuzawa (2004) argue that chimpanzees' early imitation (disappearing after week nine) can be considered an inborn ability, whereas the sporadic imitation found in juvenile and adult primates could rely on quite different mechanisms. Could a similar dissociation exist in humans? Do human neonatal imitations rely on the same mechanisms as mature, experienced-based imitations? Answering these questions would help to provide an understanding of whether neonatal imitation can be considered an inborn component of a mature MNS, or a distinct mechanism. Studies investigating the neural network underpinning imitation in newborns and older children could help to address this issue. Either way, the existence of neonatal imitation is fully compatible with our model: we do not claim that the MNS is either fully inborn or fully acquired, but that the brain is equipped with mechanisms that facilitate the acquisition of novel visuomotor associations. Indeed, neonatal imitation could facilitate Hebbian learning by increasing parents' perception of contingency with the infant, thus encouraging parental imitation of the child's facial expressions, which, in turn, might be critical for the development of a MNS for facial expressions.

Conclusions

Infants pay remarkable attention to their own actions, with a strong preference for moving hands; generate spontaneous motor activity with cyclic parameters that might be in the optimal range for Hebbian learning; and the synaptic activity in their parietal and frontal lobes synchronizes in the theta-band during grasping. This array of data, coming from a variety of empirical sources, is consistent with our hypothesis that evolution optimized infant behavioural patterns to produce canalized, reliable Hebbian learning in the parietal-temporal-frontal system. This set of behaviours and predispositions has probably not been selected mainly for the adaptive value of having a mirror system: congruent visuomotor mapping is important for motor control, and the 'symptoms' of experiential canalization we presented may have evolved primarily to optimize Hebbian learning in the motor control loop linking vision and action (Brass & Heyes, 2005; Heyes, 2001; Keysers & Gazzola, 2006; Keysers & Perrett, 2004). However, our hypothesis does not depend on the specific selective process responsible for the evolution of these mechanisms, and is broadly compatible with a range of different phylogenetic scenarios. This way of looking at the development of mirror neurons has the benefit of bringing together a body of previously unconnected aspects of infant motor and perceptual development, and provides a plausible pathway for mirror neurons to emerge from both active learning and

innate predispositions. The model proposed here is intended to have an essentially heuristic function: it is far from exhaustive, and not intended to 'prove' the absence of other significant genetic or environmental factors. Instead, we hope that it will stimulate researchers to investigate the ontogeny of mirror neurons from a novel perspective, suggest some new connections between the neural and behavioural levels of infant development, and thereby contribute to shedding light on the neural basis of social cognition.

Appendix

Model description

Our mathematical model was built around the LTP stabilization function empirically derived by Zhou *et al.* (2003). These authors reported an approximately quadratic relationship between inter-stimulus interval t and LTP stabilization (hereby ΔLTP), reaching a maximum for $t = 5$ min. The function

$$\Delta LTP = \max\{0, (20t - 2t^2)\}$$

captures this empirical relationship, as shown in Figure 3(c). In the simulations, we proceeded as follows. p was set at the beginning of the simulation; then, for each combination of λ and ϵ over a grid of values, the total LTP was set to zero and 50,000 'behavioural cycles' were run. At the beginning of each cycle, the inter-stimulus interval t_i was obtained:

$$t_i = 1/(\lambda + \epsilon_i) + t_{i-1},$$

where ϵ_i was randomly generated from a normal distribution with mean zero and $SD = \epsilon$, and t_{i-1} was the interval's previous value (starting from zero at the beginning of the simulation). Then, the 'motor pattern' was performed with probability p . If the pattern was performed, ΔLTP was calculated from t_i and added to the total LTP, then t_i was reset to zero. If the pattern was not performed, the next cycle began, thus increasing the inter-stimulus interval to t_{i+1} . After 50,000 cycles, the average ΔLTP was calculated. What we obtained in this way was the expected increase in LTP in a *single* cycle, in the context of multiple cycles; we did not attempt to model LTP saturation, as it is a virtually undescribed phenomenon. However, saturation would not change the model's qualitative behaviour.

Effects of p and ϵ on the optimal value of λ

As described in the text, increasing p leads to a decrease in optimal λ . The reason is that low p implies many 'missed' cycles, in which the motor pattern does not occur, so that the actual inter-stimulus interval increases. This effect does not depend on other assumptions in the

model. The effect of varying ϵ , on the other hand, depends on the fact that the random distribution of cycle durations

$$t_i = 1/(\lambda + \epsilon_i)$$

is modelled as being symmetric with respect to frequency. If, for example, $\lambda = .2$ cycles/min and $\epsilon = .1$ cycle/min, there is an equal probability of $(\lambda + \epsilon_i)$ being lower than .1 cycle/min (one *SD* below the mean) or higher than .3 cycles/min (one *SD* above the mean). However, the LTP stabilization function is symmetric with respect to *time*; once translated into cycle durations, the above frequency values are no longer symmetric: .1 cycles/min \rightarrow 10 min and .3 cycles/min \rightarrow 3.3 min, whereas the mean value is .2 cycles/min \rightarrow 5 min. Thus, ϵ affects LTP stabilization asymmetrically, with increases in ϵ leading to increases in optimal λ . How realistic is this effect? The CM literature usually reports frequency peaks that are more or less symmetric in shape (e.g. Figure 3a), so that the symmetry assumption may be justified, and the effect realistic; to the extent that such symmetry depends on smoothing artifacts, this effect of ϵ may be artifactual too (note, however, that to eliminate this effect of ϵ completely the frequency peaks would need to be *severely* asymmetric).

We also tested the model's dependence on the exact shape of the LTP function; to this aim, we ran simulations using either a fourth-degree polynomial or a triangular function instead of the quadratic function described above. This resulted in negligible changes in the model's output, confirming that our results hold quite independently of the details of the stabilization function. Matlab™ source code of the simulations is available from the authors.

Source of the empirical data in Figure 3c

A note on how we computed λ and ϵ from published data (Figure 3c). We relied on reported statistics when available, and approximated them from graphs when they were not available in the text. Whereas the average frequency λ was directly available in all of the studies, irregularity was always described using WHM (width at half-maximum) as a dispersion measure. Because ϵ in our model is the distribution's *SD*, we converted WHM to *SD* assuming Gaussian-shaped frequency peaks. The appropriate conversion formula is then $\epsilon = SD = (WHM/2.36)$. We plotted data from all the studies on human fetuses and infants we could find in the literature (Robertson, 1982, 1985, 1987, 1988, 1993a, 1993b; Robertson & Dierker, 1986, 2003; Robertson *et al.*, 1982). In one of the papers, CM parameters were measured before and after an experimental manipulation; in this case, we reported only the values before manipulation. In other papers, fetuses of diabetic mothers were studied on multiple occasions; in those cases, we reported only the last measurements in time, at which fetuses of diabetic mothers did not differ from those of healthy controls.

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