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Neurobiology of imitation

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Recent research on the neurobiology of imitation has gone beyond the study of its ‘core’ mechanisms, focus of investigation of the past years.. The current trends can be grouped into four main categories: (1) non ‘core’ neural mechanisms that are also important for imitation; (2) mechanisms of control, in both imitative learning and inhibition of imitation; (3) the developmental trajectory of neural mechanisms of imitation and their relation with the development of social cognition; (4) neurobiological mechanisms of imitation in non-primates, in particular vocal learning in songbirds, and their relations with similar mechanisms of vocal learning in humans. The existing data suggest that both perceptual and motor aspects of imitation follow organizing principles that originally belonged to the motor system.

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Introduction

Imitation is an important aspect of human behavior, facilitating learning and being associated with social cognition and transmission of culture [1,2]. Social and cognitive scientists have been traditionally concerned with the study of imitation. They subdivided imitation and mimicry in many different forms of behaviors associated with specific cognitive processes. An important distinction that seems to emerge from this work is between automatic mimicry of already practiced actions and imitation learning of novel actions. In the last 10 years there has also been an increasing interest in understanding the neurobiology of imitation. This article summarizes the most recent trends of the neurobiological research on imitation, following up on an article that summarized few years ago the initial investigations on the neural underpinnings of imitative behavior [3].

Before addressing the recent studies on the neurobiology of imitation, it is first useful to note that the levels of description of cognitive science and neuroscience are rather different and the constructs from one discipline cannot be easily mapped onto the other. Indeed, the neuroscience studies of imitation have largely ignored the sophisticated categorization of various forms of imitative behavior often adopted by cognitive scientists. Most of the neuroscience experiments discussed here have studied the neural correlates of relatively simple forms of imitation and imitative learning.

The initial neuroscience studies of imitation focused on identifying the ‘core’ neural systems associated with imitative behavior and their potential correlates at cellular level. After this initial wave of studies, previously reviewed [3], the studies that followed addressed many other aspects of the complex neurobiological underpinnings of imitative behavior. These more recent studies can be grouped in four major trends: first, the study of neural systems and mechanisms that do not belong to the ‘core’ imitation neural circuitry but are also important for imitative behavior; second, the study of neural mechanisms of control, for both imitative learning and the inhibition of unwanted imitation; third, investigations on the ontogenesis of the neural underpinnings of imitation and their potential association with the development of social cognition in humans; fourth, investigations on the neurobiological mechanisms of imitative vocal learning in songbirds, and their potential relations with mechanisms of vocal learning in humans. The next sections of the article will discuss each one of these research trends separately.

Neural systems for imitation: beyond the core imitation circuitry

The initial studies on the neurobiology of imitation in humans [4–7] suggested a core imitation circuitry composed of three major neural systems: the posterior part of the superior temporal sulcus (pSTS), the rostral part of the inferior parietal lobule (rIPL), and the posterior part of the inferior frontal gyrus and adjacent ventral premotor cortex (pIFG/vPMC complex). The information processing flow between these neural systems that is relevant to imitation is presumed to occur as follows: the posterior part of the superior temporal sulcus would provide a higher order *visual* processing of the observed action; this information is sent to the other two neural systems (rIPL and pIFG/vPMC complex), which are thought to form a parieto-frontal *mirroring* (both motor and visual) system. This system becomes active during action observation, action execution, and also during imitation. The mirroring mechanism that this system provides would map the observed action onto motor representations in the observer's brain.

The motor plan of the imitative action would be sent back to the posterior part of the superior temporal sulcus. Here there would be a matching process between the visual description of the observed action and the anticipated outcome of the planned imitative action. If there is a good match, the action is executed. If the match is not good enough, a correction of the motor plan is implemented [3].

At cellular level, monkey neurophysiologists have described neurons with properties that seem to fit well the proposed information processing flow described in the core imitation circuitry in humans. Indeed, the superior temporal sulcus of macaques contains higher order visual neurons that respond to the sight of intentional actions [8–11], whereas the ventral premotor cortex (area F5) and the rostral part of the inferior parietal lobule of macaques (area PF/PFG) contain mirror neurons. These cells fire during action execution and during observation of the same action or of actions that are similar and/or achieve the same goal [12–14]. The available electrophysiological data in the monkey suggest that in both parietal and frontal lobe mirror neuron areas, the 'what' of a motor act (e.g. grasping, holding, and breaking) is likely coded by individual mirror neurons, whereas the 'why' of a motor act (that is, the intention associated with it, for instance, grasping for eating or grasping for moving) is implemented by chains of mirror neurons coding individual motor acts.

How does this core imitation circuit interact with other neural systems during imitation? A functional MRI study on imitation of hand actions used independent component analysis (ICA) to identify networks of neural systems activated during imitation [15•]. ICA allows the separation of a signal depending on multiple sources into independent components. The results demonstrated four separate networks: a network of visual areas that are most likely related to the basic visual processing of the observed actions; a network of areas including both the core imitation circuit and motor areas such as primary motor cortex, supplementary motor area (SMA) and pre-SMA, cerebellum and putamen; and two additional complex networks that are most likely task-specific, that is, dictated by the specific demands of the task adopted in the study. The interesting aspect of this study is that a completely data driven analysis such as the ICA demonstrates that the core imitation circuit — which includes a purely visual neural system as pSTS — clusters with classical motor areas during imitation. This suggests that the functional processes implemented during imitation are heavily oriented toward a motor representation of the actions to be imitated, rather than toward a visual one. This is theoretically important, because it reveals that the imitation process is embodied, or anchored to the motor and body parts representations of the cortex. This suggests that it makes little theoretical sense to think about the imitation process in general, abstract terms without considering the body parts and type of actions involved.

Control neural mechanisms of imitation

Mirroring neural mechanisms may efficiently implement forms of automatic imitation but may not be sufficient for imitative learning and for the control of unwanted imitation. For instance, how does a novel action, not yet belonging to the motor repertoire of the observer, get mapped onto the motor representations of the imitator? A possible solution to this problem is as follows: Novel actions may be decomposed in simpler acts, already present as elementary motor representations in the observer/imitator's brain. This solution, however, requires the novel re-composition of the elementary motor representation to achieve efficient imitative learning. Neural mechanisms of control over the mirroring neural mechanisms previously described may be ideally placed to support imitative learning.

To test this hypothesis, an event-related fMRI study investigated the effects of learning how to play guitar chords [16••]. After practice, subjects observed both practiced and non-practiced guitar chords. Activity in the parieto-frontal mirroring system (rIPL and pIFG/vPMC complex) was higher for non-practiced guitar chords than for practiced guitar chords. A similar pattern of activity was also observed in the left dorsolateral prefrontal cortex (DLPFC). In DLPFC, activity was also higher during motor preparation for non-practiced chords, compared to practiced chords. These findings are in line with a previous brain imaging study on imitative learning that also suggested a critical role of DLPFC in imitative learning [17]. A possible interpretation of these findings is that the left DLPFC is engaged in selecting and re-combining existing, elementary motor representations in the observer/imitator's brain. If this interpretation is correct, then parieto-frontal mirroring mechanisms are also critically involved in early stages of imitative learning [18,19]. The mirroring of the elementary acts that form the novel action to be is an essential component of the imitative learning process. Such mirroring, however, is not sufficient, because it still requires the involvement of DLPFC.

A recent model, mostly based on neuronal recordings in monkeys, is compatible with this view [20••]. The model proposes a direct mirror pathway for automatic, reflexive imitation, and an indirect mirror pathway from mirror neuron areas to the prefrontal cortex for parsing, storing and organizing motor representations, all essential steps for imitative learning.

The role of the prefrontal cortex on the inhibition of unwanted imitation has been dramatically suggested in the past by the imitative behavior demonstrated in two series of brain-damaged patients [21,22]. In these patients, large prefrontal lesions were associated with the inability to inhibit imitative behavior, such that the patients would compulsively imitate the actions of other people they had just observed. The naturally occurring lesions in these patients, however, were quite large and did not suggest precise localization of the prefrontal areas actively involved in the inhibition of imitative behavior. Recent brain imaging data suggest that the anterior part of the medial wall of the frontal lobe may be critical for inhibiting automatic imitation [23]. This neural system has also been associated with reflective aspects of mentalizing, that is, attributing mental states to others. While imitation has been often associated with reflexive forms of mentalizing, its control mechanisms may have been co-opted to support reflective mentalizing [23].

Ontogenesis and relations to social cognitive development

Some rudimentary imitative abilities are present at birth in humans and non-human primates. Human, chimpanzee, and macaque infants can all imitate some facial and hand gestures [24–26]. According to a recent model, these early abilities may be supported by the direct mirror pathway that directly influences motor outputs and that develop earlier than the indirect mirror pathway [20••]. There are individual differences, however, in these early imitative abilities. A recent behavioral study in macaques performed during the first month of life demonstrates that the infant imitators (mostly imitating facial gestures) have more developed skills in goal-directed movements (reaching–grasping and hand motor control) than the infant non-imitators [27•]. These behavioral data support the notion that imitation is essential for general aspects of motor learning.

The study of the neural correlates of imitation in early human development is faced with many technical and practical challenges. For instance, brain imaging is not well suited to study awake infants, due to gross motion artifacts that cannot be corrected with current softwares. One of the best-equipped techniques of brain investigation to study the infant brain is electroencephalography (EEG) that measures the summed electrical brain activity over the scalp. Recent high density EEG studies suggest that infants as young as 6-month-old may display neural mirroring during observation of goal-directed actions [28•,29,30]. While these studies did not test imitation *per se*, its results are obviously relevant to our understanding of the ontogenesis of neural systems relevant to imitation.

Behavioral data had previously suggested a correlation between the tendency to imitate and the capacity to empathize [31]. Brain imaging data had also suggested a neural model of empathy based on activity in the core imitation circuitry, the insula, and the limbic system [32]. According to this model, activity in the core imitation circuitry would simulate (or internally imitate) the facial emotional expressions of other people. This activity would then modulate activity in the limbic system (through the insula) where the emotion associated with a given facial expression is felt by the observer. A previous brain imaging study in adults demonstrated patterns of brain activity compatible with this model [32]. A recent fMRI study on pre-adolescents measured brain activity while the children observed and imitated facial emotional expressions [33••]. The pattern of brain activity in children was very similar to the one previously observed in adults. Furthermore, the social competence and empathic predisposition of the children were assessed and were correlated with brain activity. Positive correlations between behavioral measures and brain activity were observed in the pIFG/vPMC complex, the anterior insula and the amygdala, thus suggesting that this large scale neural network for a simulation-based form of empathy and social cognition can potentially be a bio-marker of sociality.

Of birds and humans: the case of imitative vocal learning

Imitative vocal learning is a behavior that both humans and songbirds share. The neurobiology of birdsong learning was well studied — and better understood — well before the recent wave of studies on the neurobiological mechanisms of imitation in humans. The discovery of mirror neurons in monkeys and of mirroring neural systems in humans, however, has inspired a new series of studies in songbirds. The main hypothesis that these new studies tested was that some neurons in songbirds may display precise auditory-vocal mirroring. Indeed, a certain class of neurons in the swamp sparrow forebrain displays such mirroring [34••]. Certain note sequences in both the songbird's repertoire and in the birdsong of other species trigger identical responses in these neurons. When the bird sings the same sequence the same neurons display the same pattern of activity, something which is unaltered by disruption of auditory feedback. This suggests that the activity of these neurons is related to production, rather than perception of the birdsong. Importantly, the auditory-vocal mirror neurons of the swamp sparrow innervate striatal structures important for song learning, tying the activity of these cells to imitative learning.

Auditory-vocal mirroring responses have been recently reported also in the juvenile zebra finch [35•], suggesting that these mirroring responses may be widespread in songbirds. From a functional standpoint, these mirroring responses may establish a correspondence between sensory and motor codes used for communication signals. A similar concept had been proposed for human speech by the motor theory of speech perception [36–38]. Recent studies have supported the hypothesis of mirroring speech responses in humans, demonstrating activity in speech motor areas during speech perception [39,40–42]. What was lacking until recently, however, was the evidence that the activity in speech motor area during speech perception is essential to the perceptual process. A recent Transcranial Magnetic Stimulation study perturbed activity in a speech motor area while subjects performed a perceptual speech task. Speech perception was indeed impaired thus providing for the first time evidence that disrupting activity in a motor area reduces perception [43••].

A recent model on the interplay between speech motor areas and more classical auditory cortices during speech perception proposes that auditory neurons in the superior temporal cortex would provide acoustic analysis of speech sounds, whereas motor speech areas would provide a 'simulation' or 'inner imitation' of phoneme production. This simulative process would allow the prediction of the acoustic consequences of phoneme production that would be compared in the superior temporal cortex with the acoustic analysis of the heard speech sounds. If necessary, an error signal would be generated to allow correction of the simulated phoneme production used for phoneme categorization [41,44]. From a functional standpoint, this information processing flow is very similar to the one proposed in the core imitation circuitry described above.

Vocal variation does exist also in non-human primates. Group-specific variation in call structure has been reported in a number of primate species, including chimpanzees [45], barbary macaques [46], pygmy marmosets [47], and bonobos [48]. However, it is unclear whether such variation is due to imitative vocal learning. In chimpanzees, males belonging to four wild chimpanzee communities living in a similar habitat, developed group-specific pant hoots, which were not correlated with genetic relatedness [45]. The absence of genetic or habitat differences in this case provides support for the vocal learning hypothesis.

A recent study demonstrated that captive orangutan spontaneously acquired a human whistle and was able to copy a human model [49]. However, volitional control of vocal production has generally proved difficult to demonstrate experimentally in non-human primates. The growing use of functional brain imaging in great apes [50] may help settling this issue. If functional brain imaging in great apes reveals patterns of brain activity compatible with the functional model described above, then it is likely that vocal variation in great apes is due to imitative vocal learning.

Concluding remarks

Evidence from different lines of experiments suggests a common denominator with regard to the functional properties supported by neurobiological mechanisms of imitation: mirroring mechanisms may be used as forms of simulative processes that support 'forward models' of predicted sensory consequences of motor plans. The current belief is that motor control relies heavily on forward models [51]. The potential central role of forward models in imitation suggests that both perceptual and motor aspects of the imitative process are strongly anchored around organizing principles that originally belonged to the motor system.

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