Gesture in evolutionary perspective

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Abstract

Gesture is mostly a function of the upper limbs of *Homo sapiens* and is constrained by the skeleton and neuromuscular apparatus which have evolved under the selection pressures of arboreal environments. This article raises the issue of the early adaptations which determined the range of movements which made possible the emergence of gesture both technical and cultural. It addresses the problem of explaining in evolutionary terms the multi-functionality of the human hand and arm. It suggests that once early humans became bipedal further pressures combined to conserve and expand the range of adaptations afforded by the upper limbs through selection processes such as exaptation, niche construction and the Baldwin effect. It concludes that a theory of gesture must integrate evolutionary and developmental considerations.

Keywords: Evolution, gesture, bipedalism, display, thermoregulation, exaptation.

1. Introduction: a landscape without a map

Human movements, in particular movements of the upper limbs and the face, have been for a long time the object of many specialized studies, for instance, in the fields of kinesiology (e.g., Marteniuk 1976), motor neuropathology (e.g., Wallace 1989), and nonverbal communication (e.g., Kendon 1981). The term "gesture" usually refers to a subset of movements but a precise definition of what exactly constitutes a gesture has proved to be elusive (e.g., Kendon 1997, Bouissac 2002). Broader, and necessarily fuzzy definitions have been proposed (e.g., Bouissac 1973, Amstrong, Stokoe & Wilcox 1995). Kendon (2004: 12-16) offers a much less inclusive set of definitional features that focuses on the communicative function of visible actions by construing gestures proper as utterances, that is, deliberately expressive movements.

In spite of these definitional fluctuations, gesture remains the focus of a great variety of inquiries, often based on *ad hoc* definitions influenced by the background of the researchers and the nature of the investigation. Current research deals, among other topics, with the interface between language and gestures (e.g., Rausher et al. 1996, McNeill 2000), emotions and gestures (e.g., Cassell et al. 2000), the cultural relevance of gesture repertories (e.g., Mueller & Posner 2001), and the determination of which movements must be modeled in order to lend credibility to the artificial representation of speaking characters (Krenn & Pirker 2004). Many sub-domains of gesture research have come to form autonomous epistemological paradigms, with their own definitions of the object of inquiry, their own purposes and methods of investigation, and their specialized publications.

Since the notion of gesture, even in its most restricted sense, necessarily involves the complex neuro-muscular apparatus which sustains all body movements as well as the general cognitive competence which controls, represents, evaluates and appropriately uses these movements in conjunction with other activities, the investigation of gesture intersects with the concern of many disciplines. From this point of view, the neurology and pathology of gesture, the linguistic properties of sign languages, the history of gesture systems, and the psychology of nonverbal communication, to name only a few, can be considered to form sub-domains of gesture studies. Conversely, a scientific interest in gesture is included in the research agenda of mainstream disciplines such as Psychology, Sociology, Linguistics, Anthropology, Kinesiology and Neurology. As a consequence, there is a plethora of journals publishing gesture-relevant research in these domains of inquiry. For instance, *Sign Language Studies, Human Movement Science, Journal of Motor Behavior, Journal of Movement Disorder, Journal of Pragmatics, Journal for the Anthropological Study of Human Movement*, *American Journal of Speech-Language Pathology, Journal of Experimental Social Psychology*, among others, often feature articles that would qualify to appear in a journal specifically dedicated to gesture studies (e.g., Garcia 2000).

Parallel to the print media, numerous websites deal with gestures at an advanced IT level in the context of autonomous embodied agents, life-like character animation, mark-up languages and gesture input devices such as the *Gesticon* described by Krenn & Pirker (2004) or other projects such as NECA (Net Environment for Embodied Emotional Conversational Agents) and MEGA (Multisensory Expressive Gesture Applications). The above list is far from being exhaustive but illustrates the range of interests which come under the purview of gesture studies -- understood as the systematic investigation of non-random human movements, principally of the upper limbs -- each one carving out its own disciplinary niche and establishing its epistemological subculture. As it was pointed out above, there is some disagreements among researchers regarding how restricted the definition of gesture should be. The criterion of intentional communication is generally considered to be too narrow, mainly if "intentional" is taken in its psychological sense of explicit awareness, whereas most would probably judge the mere evidence of neuro-muscular organization and planning within an appropriate context as too broad a definitional feature.

However, it is generally considered that the results of these inquiries are poorly integrated into a coherent scientific paradigm and that, in spite of numerous local achievements, this general field of interest lacks a comprehensive theoretical perspective. This is not to say that theoretical views have not been formulated with respect to sub-domains such as the facial expression of emotions (e.g., Fridlund 1994), the interface of speech and gestures (McNeill 1992), the relation of sign languages to broader evolutionary considerations (e.g., Stokoe 2002) or gesture as utterance (Kendon 2004). But these efforts, which have mapped conceptually coherent domains, nevertheless form a patchwork of distinct epistemological agendas. They have yielded mostly low-level theories, that is, empirical research with typological classifications, catalogues and repertories or "dictionaries", comparisons leading to the description of cultural specifics or biological universals, patterns of developmental stages in motor and communicative competencies, and the like. There have also been a few middle-level theories, that is, generalizations bearing upon the regularities that occur between two or more sets of variables in multiple instances such as the social function of facial emotions, comparative primatology, or the hypothetical gesture origin of human language. But high-level or general theories are still missing. There is indeed a lack of a theoretical perspective within which the whole range of what is known about human movements -- including of course non-random movements such as gesture -- from biomechanics (e.g., Berthoz 2000, Vogel 2001) to semasiology (Williams 1982), would be accounted for in a comprehensive, albeit complex, manner. It should be expected from such a theory that it would be exhaustive, consistent and predictive.

The absence of such an inclusive theory -- a state of affairs that this journal has endeavored to remediate (Kendon and Müller 2001: 1-7) -- can be explained on several grounds.

The fact that there are still great difficulties in reaching a consensual definition of gestures undoubtedly comes from this theoretical lack that was earlier pointed out by Kendon (1997). Researchers must rely on dictionary entries and their etymological speculations, or, more commonly, on *ad hoc* intuitive definitions that suit their goals. The objects thus determined as the targets of empirical studies form a subset of behavioral patterns which are variously circumscribed to a body area and to a range of functions, both restrictions being influenced by the preconceptions which, unsurprisingly, are usually confirmed by the results of the research. Such circularity cannot advance our understanding of bodily movement much beyond a refinement of our perception and terminological constructions of descriptive and functional categories. But being aware of the shortcomings of a range of inquiries is only a first step. The purpose of this article is to review this state of affairs and to outline the conditions which should be met for a general theory of gesture to emerge within the context of a more general theory of human movement.

2. **Evolutionary explanations**

In any field of inquiry, what counts as a satisfactory explanation depends on the sort of practical or cognitive problems which the inquiry aims to solve. If the question bears upon the kind of relationship that holds between speech and hand gesture, any evidence of neuronal interface within an area of the brain monitored by fMRI, or any proof of dissociation obtained through neuro-pathological observations will contribute to provide an explanation by reducing the uncertainty which triggered the inquiry. In the same vein, the observation of similarities and differences of gesture morphologies and functions across populations will permit the sorting out of assumed universals and will explain diverging communicative behaviors by the same causes that are believed to account for cultural and linguistic diversity. Adaptation to the environment will then be a key notion within the conceptual framework of some anthropological theories. However, in this case, the evocation of an evolutionary principle, such as adaptation, seems fallacious because the environment in which human gestures are now observed is mostly a built environment which has been adapted to human anatomical morphology and cognitive requirement rather than the reverse. Of course, the strict Darwinism of the New Synthesis (e.g., Williams 1966; Maynard Smith 1982) and its law of natural selection can be somewhat mitigated by introducing social and artificial components of the environment as factors of selection. The so-called Baldwin effect – the fact that evolutionary changes themselves introduce novel selection constraints -- must undoubtedly be taken into consideration as a source of evolutionary pressure (e.g., Deacon 1997; Weber & Depew 2003). It has been lately brought into focus by the "niche construction" theory of Odling-Smee, Laland & Feldman (2003). But, in spite of its interest, this perspective is self-limiting in as much as it can apply only on a relatively short span of evolutionary time and must take for granted some more general evolved anatomies and neuromuscular competencies. The technological environment remains embedded within, and conditioned by the natural one and changes at its own evolutionary speed which is out of synchrony with the pace of biological evolution.

The time span of technological human cultures -- say conservatively 30,000 years -- is indeed so minute with respect to the evolution of hominins -- in the order of several million years -- that the artificial environment is more likely to impact upon the development of humans and their social ranking than their anatomic evolution proper. This is fortunate because if some human populations had, for instance, evolved a specific anatomy in response to the domestication of the horse, this branch would now probably be already extinct. It is bipedalism and the capacity of running fast which made the domestication of the horse possible, as well as, much later, the exploitation of the wheel in the bicycle. The understanding of the evolution of bipedalism, that is, of what adaptation preceded it and why it changed, has more explanatory value than the description of developmental processes and local adjustments (Walker & Shipman 2005, Bramble & Lieberman 2004).

Only evolution by natural selection can afford true explanations, or, at least, explanations that embrace the largest number of phenomena which can be related to each other within a unifying timeframe of great magnitude. Paleontology, and all the dating technologies it spawned over the last two centuries, marked the beginning of human thinking beyond historical time (Zimmer 1998). Understanding gestures first requires an evolutionary understanding of the primate limbs and the cobbling together, through natural selection, of the complex, actually messy, skeletal and neuromuscular apparatus which enables technical and communicative gestures as subsets of more complex survival behaviors. Understanding gestures cannot only consist of describing chains of interconnected reflexes and the particular actions they make possible but must conceptualize the kind of functions they were driven to implement by natural selection. In other words, each step in their emergence must be conceived as a kind of photographic negative of the environmental constraints which selected across time the features which are combined in their overall adaptation. This view does not imply that the whole system obeys a preconceived plan, a blueprint which would have, from the beginning, taken into consideration a range of functions which it was designed to serve. Indeed, when we deal with gestures and the anatomical apparatus that sustains them, identifying a “beginning”, a starting point, would be a daunting, in fact impossible task, if only because there cannot be a single point of origin for any organ but rather many distributed factors from which viable patterns emerged through natural selection in the context of whole organisms and populations. A variety of evolutionary pressures can converge toward morphologies with a variety of functions. Efficiency for survival in a particular environment is the key, rather than the overall consistency of the design. Old morphologies can be co-opted by new emergent functions when the context is modified, a phenomenon which some evolutionists call “exaptation”. Such a theoretical frame must be considered for understanding the human arm and hand. Appendages, limbs and digits are not confined to primates, not even to mammals. The evolutionary snapshot of the last two million years can be understood only if assessed with respect to a much deeper anatomical “history”.

There are, of course, several levels of understanding and the chronicle of scientific knowledge documents epistemological controversies which are often reducible to *top-down* versus *bottom-up* approaches. Both have led to partial understandings of natural phenomena. Gestures can be studied at the synaptic level as does the current research on “mirror neurons” (e.g., Stamenov & Gallese 2002). Another epistemological strategy is to adopt David Marr’s epochal method to understand the mammalian vision system (Marr & Poggio 1976, Marr 1982, Glimcher 2003: 133-144). In order to understand a biological architecture, one must first understand what this architecture makes possible, or, in other words, what is its adaptive value. Through a form of reverse engineering, the strategy consists of starting from the top by describing as formally and mathematically as possible what the system does or tries to do, and then asking how the necessary computation is done by the biological hardware, thus opening a window on the successive selections from which the system has emerged. This must be done while keeping in mind that a system that evolved in response to a certain range of pressures may happen to offer a serendipitous pre-adaptation in the face of new environmental challenges. The hypothesis developed in this essay is that such considerations allow one to frame the problems raised by the semiotics of gestures within a perspective which explains many puzzling aspects of human upper-limb movements, in particular their poly-functionality as well as, paradoxically, their probable obsolescence in the long term as it was suggested by prehistorian Leroi-Gourhan (1993).

3. **From appendages to limbs**

The evolving of appendages is a common feature in the history of life on earth. Spikes, antennas, filaments, and other extensions of the exo- or endoskeleton, or of the skin envelop, can indeed provide advantages such as protection from predators, adherence to desirable locations, improved control of mobility, camouflage and the like (e.g., Siveter et al. 2001). Although essentially passive, these extensions of the organism itself confer some benefits in appropriate environments. All the more so since they are usually dispensable and often can grow again if they get broken or eaten. When appendages acquire some form of articulation and muscular autonomous control or become integrated under the control of a central neurological system and permit specific adaptive behaviors coordinated with vision or other sources of relevant information, they are called limbs (e.g., Blaxter 2001, Dickinson et al 2000). This active functionality preserves at the same time certain advantages, as well as liabilities, of mere appendages in as much as limbs remain to a lesser or greater degree expendable. If all appendages are not limbs proper, all limbs are appendages and carry both the benefits and the costs of the latter. For instance, in warm-blooded animals they may contribute to the thermoregulation of the circulatory system. But they are also prone to being grasped by predators as they are more exposed than the rest of the body. Their loss, however, does not necessarily means loss of life although some limbs are more vital than others because of the functions they have come to serve.

Instead of evolving into limbs, appendages can evolve as ornaments in species in which the females select among the males the fittest individuals for reproduction. This evolutionary process is known as the "handicap principle" (Zahavi & Zahavi 1997). It contends that males who can demonstrate their fitness in spite of being loaded with costly (and dangerous) appendages such as extra-long feathers or dysfunctionally large antlers, horns or tusks get a better chance at spreading their genes. Such intra-specific semiotic arms races seem to have contributed to the evolution of maladaptive phenotypes in some species that led them to extinction. In any case, appendages always constitute a risk which may pay off but is at the same time double-edged.

Insects present a rich repertory of limbs which are used for climbing, swimming, running, feeding, spinning, grooming, fighting, signaling, etc., with a vast range of adaptive devices regarding the modality of contact with surfaces (e.g., cupping, hooking) and the source of motility that can be molecular (Vale & Milligan 2000) or supra-molecular (e.g., springs and ratchets) (Mahadevan and Matsudaira 2000). Instances of the handicap principle are also well attested by entomologists in the competition for reproduction (Choe & Crespi 1997). The importance of limbs in copulation behaviors is not less obvious among insects than in mammals, as it has been provocatively illustrated by Marjorie Leggitt in entomologist James Wangberg's fascinating account of "the erotic lives of bugs" (2001).

This brief excursus into another realm of life was designed to put mammalian limbs, more specifically primate limbs in their proper evolutionary context, that is, among the devices which were selected over time as solutions to problems of survival and reproduction with respect to particular environment constraints.

Although there are still some gaps in the fossil record, the paleontology of fishes and early tetrapods allows us to trace back the evolutionary transition from fish to air-breathing, four-legged land vertebrates some 370 millions years ago, when fins evolved into limbs (Clark 2002, 2004, Langdon 2005). The fossil record documents the steps through which an appendicular skeleton provided a scaffold for limb musculature (Neyt et al. 2000), an adaptive process which does not appear to have been initially constrained by movement on land although tetrapods were at an advantage whenever the ability to move on land became an asset. Carl Zimmer (1998) has summarized in his well-informed popularization of the tetrapods saga not only the state of knowledge which had been reached in the mid-1990s but also the way in which paleontological data collecting and reasoning proceed. His account interestingly, albeit marginally, bears upon the evolution of digits, a very common phenomenon which is observed across taxa and represents a great variety of adaptive solutions.

The common ancestors of apes and humans were tree-dwelling mammals who had evolved tactile, grasping and balancing abilities as well as the color vision and sense of perspective adapted to arboreal life (Walker & Shipman 2005). In 2001, a multidisciplinary conference involving both paleontologists and molecular biologists addressed the question of primate origins and adaptations. The evidence presented there suggests an early versatility of movements and advanced eye-gesture coordination (Moffat 2002). The evolution of the primate hand, with its characteristic power and precision grips, has been the object of intense scrutiny bearing on its anatomy, neurophysiology and functions (e.g., Goodwin & Darian-Smith 1985, Jeannerod 1988, Lewis 1989, Landsmeer 1993). Tree-dwelling primates feeding on insects, leaves, fruits and nuts while keeping their balance on tree limbs or hanging from branches, in addition to grooming, courting, fighting and nurturing, had their hands full, so to speak. Arboreal ecology implies a range of constraints which have molded the early physical and cognitive abilities of primates. Many of these evolved competencies have been conserved in most monkeys and apes, sometimes as the very basis of their existence, sometimes simply making possible alternative ways of life for moving, resting, or hunting. In humans, environmental circumstances can rather easily revive vestigial capacities that enable survival strategies exploiting the resources of trees for escaping danger and providing nutrition. Some sport and circus acrobatic specialties display, in a spectacular mode, a range of ancestral survival behaviors such as climbing vertical poles, balancing on minimal surfaces, or grasping, and hanging from, bars thanks to the power grip of the hands. A hardwired grip-reflex is well documented in human neonates and even in the absence of any visible support an adult who trips or loses his/her balance tends to spontaneously produce a grasping gesture. Recent vistas on the anatomical evolution of *Homo* can be found in Walker & Shipman (2004) and Langdon (2005).

In evolutionary time the emergence of brachiation – that is, the dependence on suspension by the arms for locomotion -- is relatively recent and the evolutionary pressures which fine tuned the primate arms and hands have been, to some extents, perpetuated in bipedal humans' artifactual environment, built with more or less direct reference to tree-structure models. If the hand appears to be so well adapted to the technological environment, it is essentially because this environment has been built by the hand in view of its reaching and manipulating capacities but these capacities themselves have evolved with respect to the earlier constraints of arboreal life.

4. From limbs to gestures: the social exploitation of gesticulation

Based on the evidence of paleontology, the generally accepted narrative of human evolutionary origins claims that some primate ancestors adopted a terrestrial way of life under hypothetical circumstances that range from demographic pressures to habitat and climate changes. The various hypotheses that have been proposed in order to account for bipedalism are summarized and discussed in Langdon (2005: 116-128). Most suggest that bipedalism was selected by a new environment in which it was advantageous to see farther and run faster with staying power. The anatomical and physiological transformations triggered over time by these new constraints have been amply discussed in human paleontology literature and have been incorporated into arguments concerning the emergence of physical and cognitive abilities specific to modern humans. Some earlier evolved competencies of the common ancestors of apes and humans have obviously been conserved, often through recycling or exaptation, sometimes called pre-adaptation, before being further modified within a limited range of adaptive variations.

If the above scenario is accepted, it would follow that *Homo erectus* inherited two upper limbs that had become partially obsolete in as much as the arboreal environment which had fashioned them was not any longer totally relevant to hominid survival. Several functions of course remained fully served by the visuo-motor complex formed by the arms, hands and eyes, such as accurately reaching and aiming, selecting appropriate food, carrying it to the mouth, catching or fending off pestering insects, self- and mutual-grooming, caring for infants and other similar behaviors which have to be efficiently performed whether one is in a tree or on the ground. However, it would seem that bipedal terrestrial locomotion leaves the upper limbs idle for a fairly large portion of the waking time with a range of potential movements far exceeding the immediate survival needs. Evolutionary comparative anatomy has detailed the differences in the length of bones, joints morphology, adjustments between the facets of the articulations and the range of movements that characterize modern humans with respect to their predecessors and to the Neanderthals, as well as to other primates (e.g., Lewis 1977, Villemeur 1994). Rather than demonstrating design optimality the human hands is a conservatory of past adaptations – a phenomenon called "mosaic evolution" with different parts evolving at different rates -- which have been for a large part recycled for new functions while carrying at the same time the burden of history. It constitutes one of the many examples of the unpredictable tinkering of natural selection.

The emancipation of the upper limbs from the constraints of arboreal or quadrupedal terrestrial locomotion has been held responsible for most of the distinctive features of *Homo* and the subsequent emergence of *Homo sapiens*. Among these features is the rich repertory of communicative gestures, considered by some as the crucial stepping stone to articulate language (e.g., Corballis 2002). It is however epistemologically unsound to attempt uni-linear reconstructions of evolutionary causes and effects because such hindsight artificially carves out sequences on the model of a teleological process and thus irresistibly construes evolution as an agency implementing a preconceived design. In order to try to escape this tautological explanation of the hand by itself (viz. Michelangelo's representation of the creation of man), let us consider, heuristically, the conservation of hominid upper limbs as a fluke, and let us imagine the complex context which may explain why these two lateral appendages under cortical control were not only preserved but eventually influenced directly evolution itself.

Focusing on the evolution of the limbs is of course an artifact of argumentation. In spite of the fact that limbs are relatively expendable, it makes no sense to conceive of the hands, for instance, independently of the whole neuro-motor and cognitive apparatus and its multimodal processing and coordination. Since the brain does not fossilize, most knowledge on its evolution must be inferred from the gross superficial anatomy which is revealed by skull endocasts and the inferred global capacity of the cranium. Many hypothetical evolutionary changes based on neuro-anatomy have been proposed on the ground that they must be implied by the changes in the material productions of *Homo* which are found in the archeological record. These inferences are made of course in view of whatever is known, at the time they are made, about modern brain architecture, physiology and development. The issue of the evolution of gesture, in the primal sense of both the creative transformation of objects and their virtual manipulation during speech, is coterminous with the issues of the evolution of symbolism which sustains gesture's communicative functions and pertains, more generally, to the cultural patterning of bodily movement and its preservation, albeit with possible modifications, over time. But this evolution could take place only once the forelimbs had proved to be adaptive for a bipedal terrestrial mode of life although not quite under the same selective constraints as those which prevailed in an arboreal environment. Therefore, it is important to examine these new adaptations not only because they have most likely persisted in modern humans but also because they are the prerequisite for the evolution of the elaborate movements that characterize social gesture in their communicative and ritualistic functions.

The tentative hypothesis that is proposed here is that the adaptive value of the upper limbs was preserved, or even perhaps enhanced, through at least two natural selection pressures, one purely physiological, the other of a more socio-biological nature. Both, of course, equally pertain to the reproductive success of individual phenotypes.

The former comes from the advantage of an efficient thermoregulation system mainly for an organism which probably came to rely on distance running for catching prey in a savannah environment (Bramble and Lieberman 2004). From this point of view, arms can be viewed as offering an increased surface for cooling through evaporation, a solution to the problem of overheating similar to the elephant ears whose morphology and dynamic have little to do with hearing. The agitation of the arms while running still serves this function by accelerating the evaporation rate of the transpiration that accompanies exertion, but even more obvious is the spontaneous reliance on the hands to create cooling drafts close to the face and neck when the ambient temperature gets too elevated or when stress causes overheating and perspiration. This function of the forelimbs can be technologically amplified by handheld fans. It could even be hypothesized that the intense gesticulation that usually occurs during heated discussions can be accounted for at least in part by this thermoregulatory function. Such hypotheses are falsifiable since they could be tested in appropriate experimental settings both in laboratory conditions and by mapping the geographic distribution of gesticulatory intensity.

The second evolutionary pressure that could be identified as an explanation for the early maintenance of the forelimbs belong to the category of handicap (Zahavi & Zahavi 1997) through which males compete to display outstanding fitness. Well controlled gesticulation effectively conveys prominent musculature (which, often, in urban modern setting is not functional) and creates an impression of increased body height and volume along particular corporal outline. It also contributes to establish and secure increased personal peripheral space. This kind of natural selection would be congruent with the evolution of bipedalism (an intra-specific display commonly observed in mammals) and the subsequent reliance on distal vision as well as the selective development of neuro-visuo-motor coordination. It would be even possible to go as far as grounding the selection of gestural imitative competence on competitive display with variations. This would perhaps account for the fact that most human cultural (artistic) productions, most of which developed from courtship rituals, exploit the upper limbs which afford more compositional freedom than the lower limbs whose primordial functions of support and locomotion are ever present and demanding. Gait is obviously more constrained than gesticulation.

Of course, the two evolutionary factors which have been tentatively sketched above as having contributed to the maintenance of the basic anatomy of the forelimbs of *Homo* once it became bipedal are not the only ones. Others previous adaptations remained advantageous whether in trees or on the ground albeit with some strategic adjustments. The reason for which this two-pronged hypothesis has been emphasized is that it could provide a robust evolutionary transition toward object manipulation, gesticulation and gesture, and ultimately toward symbolism. Such a transition is a prerequisite for the opportunistic exploitation of the communicative potential of the upper limbs and for other cultural developments, including the spreading of gesture patterns across generations and through populations.

5. **Conclusion: The evo-devo of gestures**

Evolutionary explanations are, however, more or less clever arguments that strive to overcome the reproach of being just-so stories based on anecdotal evidence. If the understanding of culturally patterned bodily movement is to go beyond the mere description of the morphologies and functions of somewhat arbitrarily defined local domains of experience, the inquiry into the evolution of gesture is bound to encounter the evo-devo epistemological challenge, that is, to formulate a theory that can integrate into a single perspective evolutionary and developmental models of human functional and symbolic (i.e., communicative) movements. It is important to note the remarkable continuity of the basic way in which limbs are made across taxa. In vertebrate limbs, the basic skeletal architecture is always the same. Adaptations to diverse functions such as swimming, running, flying, digging, grasping and the like are morphogenetic variations on the same fundamental theme (Duboule 1994). Advances in molecular biology shows that limb developments in vertebrates and insects are basically the same (Martin 1995). How does limb and gestural specialization occur through development? How hardwired are some patterned movements and their interpretation by conspecifics? How plastic and flexible can dynamic behavior be? To what extent can cross-specific mimicry, copying or imitation overwrite evolutionary and developmental programs? To what degree may such overwriting be adaptive? These are questions that an evo-devo theory of gestures should answer, thus opening a vista on the way the gestural competence of each individual is rooted not only in his/her proximal history but also in a long evolutionary lineage which explains the possibility of this history.

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