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). Current research deals, among other topics, with the interface between language and gestures (e.g., McNeill 2000), emotions and gestures (e.g., Cassell et al. 2000) and the cultural relevance of gesture repertories (e.g., Mueller et al. 2001). 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. There is a plethora of journals publishing research in these sub-domains. 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 gestural input devices.The above list is far from being exhaustive but illustrates the range of interests which come under the purview of human movement studies, each one carving out its own disciplinary niche and establishing its epistemological subculture.

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), or the relation of sign languages to broader evolutionary considerations (e.g., Stokoe 2002). But these efforts have yielded mostly low-level theories, that is, empirical research with typological classifications, 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, 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 an inclusive theory of gestures 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 (Kendon 1997). Researchers must rely on dictionary entries and their etymological speculations, or, more commonly, on *ad hoc* definitions that suit their goals. The objects thus determined as the targets of empirical studies form a subset of dynamic 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 human dynamic behavior 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 gestures to emerge.

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 cultures will permit the sorting out of assumed universals and will explain diverging communicative behaviors by the same causes that are believed to account for ethnic 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 certainly must be taken into consideration as a source of evolutionary pressure (e.g., Deacon 1997; Weber and Depew 2003). It has been lately brought into focus by the "niche construction" theory of Odling-Smee, Laland and 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 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 *Homo* -- in the order of several million years -- that the artificial environment is more likely to impact upon the cognitive development of humans and their social ranking than their biological 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 (Bramble and Lieberman 2004).

Only macro-evolution 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 putting together, through natural selection, of the complex, actually rather 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 adaptive properties. 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 "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 and Gallese 2002). Another epistemological strategy is to adopt David Marr's epochal method to understand the mammalian vision system (Marr and 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.

3. **From appendages to limbs.**

The evolving of appendages is a common feature in the history of life. Spikes, antennas, filaments, and other extensions of the exo- or endo-skeleton, 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 confer some benefits in congruent 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 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 cooling of the circulatory system. They are also prone to being grasped by predators as they are more exposed than the rest of the body, but their loss 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 and 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 dysfunctional oversized antlers, horns or tusks get a better chance at spreading their genes. Such intra-specific semiotic arm races seem to have contributed to leading some species 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 and 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, fourlegged land vertebrates some 370 millions years ago, when fins evolved into limbs (Clark 2002, 2004). 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 marginally bears upon the evolution of digits, a very common evolutionary phenomenon which is observed across *taxa* and represents a great variety of adaptive solutions.

The common ancestors of apes and humans were tree-dwelling tetrapods who had evolved tactile and grasping abilities as well as efficient color vision adapted to arboreal life. 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 and 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.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.

In macro-evolutionary time the emergence of brachiation is relatively recent and the evolutionary pressures which fine tuned the primate arms and hands have been, to some extents, perpetuated in bipedal humans' artificial 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 constraints of arboreal life.

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

Based on paleontology evidence, 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 climate changes. Bipedalism would have then been selected by an new environment in which it is advantageous to see farther and to 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 ensue that *Homo erectus* inherited two upper limbs that had become partially obsolete in as much as the 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, 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, relations 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 which have been for a large part recycled for new functions. It constitutes one of the many examples of the unpredictable tinkering of natural selection, a kind of historical accident which, literally, changed the face of the earth.

Emancipation of the upper limbs from the constraints of locomotion has been held responsible for most of the distinctive features of hominids 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 articulated language (e.g., Corbalis 2002). It is however epistemologically unsound to attempt linear reconstructions of evolutionary causes and effects because such hindsight artificially carves out sequences on the model of a kind of "chaîne opératoire" and thus irresistibly construe 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 endocasts and the 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 artificial productions of *Homo* which are found in the archaeological 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 gestures, in the contemporary sense of the term, is coterminous with the issues of the evolution of symbolism, and pertains both to the cultural patterning of dynamic behavior and its preservation, albeit with possible modifications, over time.

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

The former comes from the necessity of cooling the circulatory system mainly for an organism which came to rely on distance running for catching preys (Bramble and Lieberman 2004). From this point of view, arms can be viewed as tubes offering a maximal surface for cooling 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 (gesticulation) still serves this function, often technologically amplified by handheld fans.

The latter evolutionary pressure would belong to the category of handicap (Zahavi and Zahavi 1997) through which males compete to display outstanding fitness. Well controlled gesticulation effectively conveys prominent musculature (which often 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 the neurological coordination of vision and movement. It would be even possible to go as far as grounding the selection of gesture imitative competence on competitive display with variations. This would perhaps account for the fact that most human cultural (artistic) productions 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 thus probably more constrained than gesticulation. This two-pronged hypothesis would provide, it seems, a more robust basis for the conservation of the morphology of the upper limbs than the communicative potential and other cultural developments (including the spreading of memetic motor algorithms through populations of gesture patterns) which, then, could be construed as secondary exploiting of an apparatus whose cost is high but adaptive for the two reasons listed above, and which, at the same time, is not utilized 100% of the time. From this theoretical basis all the diverse functions of gestures, including the cultural emergence of (social and religious) rituals and their memorization, could be naturally derived and explained in an evolutionary perspective.

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 patterned dynamic behavior is to go beyond the mere description of the morphologies and functions of somewhat arbitrarily defined local domains of experience and their integration into the grand evolutionary narrative of macro-evolution, the inquiry into gestures 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 limb and gesture specialization occur through development? How hardwired some patterned movements and their interpretation by con-specifics are? How plastic and flexible dynamic behavior can be? To which extent cross-specific mimicry, copying or imitation can overwrite evolutionary and developmental programs? To which degree such overwriting may be adaptive? These are questions that an evo-devo theory of gestures should answer.

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