Plasticity, innateness, and the path to language in the primate brain

Comparing macaque, chimpanzee and human circuitry for visuomotor integration

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Many researchers consider language to be definitionally unique to humans. However, increasing evidence suggests that language emerged via a series of adaptations to neural systems supporting earlier capacities for visuomotor integration and manual action. This paper reviews comparative neuroscience evidence for the evolutionary progression of these adaptations. An outstanding question is how to mechanistically explain the emergence of new capacities from pre-existing circuitry. One possibility is that human brains may have undergone selection for greater plasticity, reducing the extent to which brain organization is hard-wired and increasing the extent to which it is shaped by socially transmitted, learned behaviors. Mutations that made these new abilities easier or faster to learn would have undergone positive selection, and over time, the neural changes once associated with individual neural plasticity would tend to become heritable, innate, and fixed. Clearly, though, language is not entirely "innate;" it does not emerge without the requisite environmental input and experience. Thus, a mechanistic explanation for the evolution of language must address the inherent trade-off between the evolutionary pressure for underlying neural systems to be flexible and sensitive to environmental input vs. the tendency over time for continually adaptive behaviors to become reliably expressed in an early-emerging, canalized, less flexible manner.

Keywords: action perception, tool use, white matter, diffusion tensor imaging, superior longitudinal fasciculus, dorsal stream, evolution, chimpanzees, macaques

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Introduction: Comparative neuroscience, exaptation, and language

Early attempts to study the evolution of human-specific abilities like language focused on adaptations that exist in humans but not other animals. For example, Brodmann's famous cytoarchitectonic maps – which he produced in both humans and other species – show an area 45 only in humans, reflecting the notion of human-unique anatomy underlying human-unique cognitive function. Notably, area 45 and 44 homologues have now been established in non-human anthropoid primates (e.g., Petrides, 2005; Schenker et al., 2008). Paralleling this anatomical perspective, earlier behavioral/cognitive perspectives on language evolution focused on innate, "hard-wired" abilities – e.g., Chomsky's "universal grammar." In contrast, current perspectives are oriented more toward continuity, asking how human-unique functions were derived or exapted from pre-existing functions relying on pre-existing structures. Increasingly, research indicates that the evolution of vision-for-action circuitry is at the root of a suite of interrelated human specializations that all rely on capacities for complex social learning and cumulative culture, including language. This paper reviews comparative neuroscience evidence on the evolutionary timecourse of these adaptations, and considers theoretical explanations for how new functions can emerge from pre-existing circuits.

We cannot directly observe our own history, but we can extrapolate it via comparisons with our extant primate relatives. Humans' closest living relatives are chimpanzees; our ancestors and theirs diverged about 6–7 million years ago (Goodman et al., 1998). Humans are more distantly related to Old World monkeys, such as macaques, with our last common ancestor existing about 25–32 million years ago (Goodman et al., 1998). Comparative neuroscience draws conclusions about human evolution in the following way. If a trait exists in multiple extant primate species, it is assumed to have existed in their last common ancestor. Conversely, if a trait exists in one group of related species but not a more distantly related outgroup, it is assumed to have emerged after their divergence. This approach allows for the extrapolation of the evolutionary history of brain adaptations.

LCA-m: Early primate adaptations for the visual control of action

Primates share a distinctive elaboration of cortical machinery for visuo-manual integration that is perhaps their quintessential brain adaptation. Early primates were diurnal, arboreal animals who made a living by hunting insects and fruit in the fine terminal branches of trees (Sussman et al., 2013). Success in this niche was supported by the emergence of ventral premotor cortex, which allowed for the integration of visual input with new, higher-order control of sequences of actions, and area MT (or VS), a specialized retinotopic motion-processing region. PMv and MT are present in all primates (Kaas, 2012); thus, the basic action-processing adaptations that later became exapted for social and cultural learning were in place at or near the phylogenetic root of our clade. Given that Old World monkeys, New World monkeys, and great apes (including humans) all show evidence of a mirror system (although note that direct electrophysiological observation is limited to macaques and humans, whereas chimpanzee evidence comes from neuroimaging studies (Hecht et al., 2013)), it is likely that mirror neurons were also present in our earliest ancestors, and may develop spontaneously across phyla via general Hebbian learning mechanisms in cells with access to both motor and sensory information. Additionally, both New World monkeys (capuchins) and Old World monkeys (macaques), like humans, can recognize when they are being imitated and show preferences for individuals who imitate them (Chartrand & Bargh, 1999; Paukner et al., 2009; Sclafani, et al., 2015), indicating that some degree of awareness about the correspondence between one's own and others' actions and a subsequent link to affective or motivational processing may have also been present very early in primate evolution.

From the emergence of MT and PMv in early primates, further neural adaptations evolved, as evidenced by the presence of these features in the brains of extant anthropoids. Visual processing of motion expanded from MT into the dorsal visual stream, a network of linked regions extending from extrastriate occipital cortex into posterior parietal cortex (Goodale and Milner, 1992). The dorsal stream processes "how" observed events unfold and is involved in the on-line control of action. Its functions are dissociable from, but interconnected with, those of the ventral stream, which extends from extrastriate cortex into the lateral and inferior temporal lobe. In contrast to the dorsal stream, the ventral stream processes "what" is observed in the periphery, including the recognition of objects, individuals, and body parts. Both streams are present in modern macaques, chimpanzees, and humans. The ventral visual stream has clearly undergone important evolutionary change, such as the emergence of semantic cortex and specialized modules for face processing. However, we argue that multiple, successive adaptations to the dorsal stream were especially important for the evolution of behavioral products of complex social learning and cumulative culture, including language and tool use (E. Hecht, 2016).

LCA-c: Hominid dorsal stream adaptations for social transmission of learned skills

Several adaptations for the social transmission of learned skills appear to have occurred after hominids (humans and other great apes) diverged from monkeys. While primates in general are skilled social learners, there are species differences in what *kinds* of behaviors are socially transmitted. Chimpanzees and orangutans, like humans, spontaneously and flexibly use tools in the wild, and tool use skills are transmitted socially (Gruber et al., 2012; Inoue-Nakamura & Matsuzawa, 1997). Gorillas also show skilled, hierarchically-complex, socially transmitted object manipulation abilities (e.g., leaf folding, Byrne et al., 2011). Bonobos have not yet been observed to typically use tools in the wild, but are capable of doing so in a laboratory context without training (Roffman et al., 2015). In contrast, monkeys have not been found to show clade-wide endemic capacities for tool use, although important exceptions do exist, as discussed later. The fact that some monkeys do use tools suggests that the neural precursors for tool use could be endemic in anthropoids, which may only evolve into a fully functional species-typical behavior given specific selection pressure. However, the abundance of tool use and gestural communication in great apes, compared with the clearly reduced complexity of these behaviors in monkeys, suggests that the neural mechanisms involved in tool use and gestural communication may have mainly become elaborated after hominids diverged from Old World monkeys, before modern hominid species diverged from each other.

There are also species differences in which *aspects* of observed behaviors have been shown to be socially transmitted. A broad, simplified distinction can be made between emulation, or behaving in a way that results in reproducing the outcome of an observed action (even though the specific behavioral sequence might be different), versus imitation, or additionally copying the specific methods used to achieve the result (Whiten et al., 2009). Monkeys, to date, are not known to imitate, or may do so only in specialized, limited contexts (Visalberghi & Fragaszy, 2002). However, chimpanzees can imitate in certain circumstances, namely when the causal relationship between an actions' movements and its result is not perceptible (Homer & Whiten, 2005). Chimpanzees also show limited but measurable success at reproducing arbitrary movements (Hayes & Hayes, 1952) and are capable of miming goal-directed actions in the absence of objects or actual goals (Marshall-Pescini & Whiten, 2008). This suggests that the capacity for imitation may have been present in the brains of early hominids.

This wide variation in the capacity for imitation has stimulated not only the quest to better characterize the behavioral variation but also for neuroanatomical correlates. Following the divergence of hominids (apes and humans) from monkeys, there appears to have been a shift in the general distribution of white matter connections within long-range circuitry for performing and observing action. In macaques, ventral-stream temporal regions involved in the perceptual processing of objects and biological motion project mainly to inferior frontal cortex, following a ventral route through the inferior longitudinal fasciculus and extreme/external capsules; a relatively small proportion of the network connectivity travels dorsally through inferior parietal cortex (Hecht et al., 2013; Petrides & Pandya, 2002, 2009). In chimpanzees, though, this dorsal route through the middle and superior longitudinal fasciculi into frontal cortex became more pronounced, and in humans, these dorsal connections are even more robust (Hecht et al., 2013). These comparisons used diffusion tensor imaging data, which does not image white matter at the cellular level, and it is not yet fully understood what cellular variables may affect this type of quantification. Still, though, it seems that in monkeys, most of the information that inferior frontal cortex receives about observed events comes from the ventral visual stream, whereas in apes, inferior frontal cortex receives a relatively greater input from the dorsal visual stream. This progression of structural differences parallels a progression of functional differences: ventrolateral prefrontal responses to observed objects are greater in macaques than in humans (Denys et al., 2004). Similarly, ventrolateral prefrontal responses to observed object-directed grasping are greater in chimpanzees than humans (Denys et al., 2004). Given that prefrontal cortex is generally engaged with higher-order representations of actions and visual scenes, whereas earlier visual regions contribute feature-level processing, this may reflect a general trend toward increased processing of bottom-up perceptual details of observed actions, as opposed to primarily top-down cognitive representations (Hecht et al., 2013).

Additionally, new functional regions emerged in inferior parietal cortex after humans' and chimpanzees' last common ancestor with macaques. For example, 3D form-from-motion stimuli activate the intraparietal sulcus in humans but not macaques (Vanduffel et al., 2002). Similarly, observed tool use activates the anterior supramarginal gyrus in humans but not in macaques (Peeters et al., 2009). We do not know how chimpanzee inferior parietal cortex might respond to these types of stimuli because the relevant experiments have not been performed. These evolved functional adaptations in parietal cortex are likely supported by underlying structural differences. Macaques show little or no connectivity between the anterior supramarginal gyrus and inferotemporal object processing cortex (Rozzi et al., 2006; Zhong & Rockland, 2003), whereas diffusion tensor imaging studies in humans and chimpanzees indicate that these connections are readily measurable (Hecht et al., 2013). We have postulated that these new connections may allow for integration between feature-based object processing in inferotemporal cortex and kinematic-spatiotemporal processing in parietal cortex (Hecht et al., 2013), a function that may be important for both individual and social learning of manual action, potentially including gesture and/or tool use.

This shift in the distribution of structural connectivity may also confer different response properties to the mirror system. In macaques, frontal mirror neurons seem primarily responsive to transitive actions for which the object toward which the actions are directed is visible or has very recently been visible (Umiltà et al., 2001) and have been reported to respond not at all (Rizzolatti et al., 1996) or very little (Kraskov et al., 2009) to observed movements which lack physical goals on objects (intransitive actions). In contrast, when chimpanzees observe others' actions, these are mapped onto nearly identical voxels as the chimp would use to produce those same movements itself, regardless of whether they produce a physical result on an object (Hecht et al., 2013). Humans also show highly specific mapping of intransitive action onto one's own motor system (Kraskov et al., 2009). This suggests that the neural capacity to simulate not only the goals of others' actions, but also the individual component movements, evolved before humans and chimpanzees diverged – potentially coincident with the capacity for imitation and the perceptual comprehension of non-object-directed manual actions, although it seems clear that humans far out-perform other apes in this domain, as discussed in the next section.

Human-specific adaptations: Integrating cognitive control and action sequencing with high-fidelity representations of action details

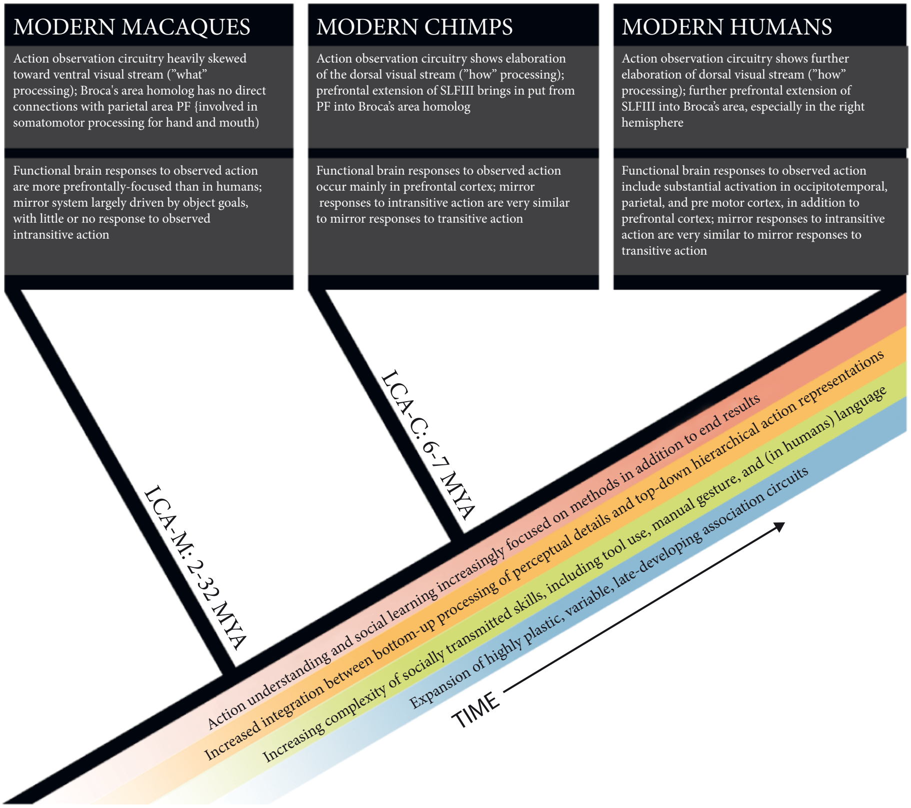
It appears that the evolutionary trend toward increased bottom-up processing of actions' perceptual details continued not only past the monkey-ape divergence but also past the chimpanzee-human divergence. Whereas chimpanzees are capable of imitation but behaviorally biased toward emulation, humans show a strong inclination toward imitation, even extending to over-imitation, or reproduction of action details that are not causally related to achieving the end goal (Whiten et al., 2009). Performing actions in a recognizably similar way to particular individuals or groups clearly plays an important socio-communicative role in human interaction; humans spontaneously and subconsciously imitate behaviors like body posture and speech patterns in a way that reflects social status (Chartrand & Bargh, 1999). In addition to greater attention to the details of others' actions, humans also show greater attention to the movement details of their own actions. For example, chimpanzees find it difficult to differentiate their own cursor from one controlled by the computer, if both are achieving the same end goal (Kaneko & Tomonaga, 2012).

Several neural adaptations may underlie this continued shift. For example, during the simple, passive observation of object-directed reach-to-grasp actions, most of the regional cerebral glucose metabolism in the chimpanzee brain occurs in prefrontal cortex, whereas human brains show a more distributed pattern of energy expenditure across of occipital, temporal, parietal, premotor, and prefrontal cortex; chimpanzees show significantly greater activity in ventrolateral prefrontal cortex, while humans show significantly greater activity in inferior parietal, inferotemporal, and ventral premotor cortex (Hecht et al., 2013). In this respect chimpanzees are similar to macaques, which show greater glucose metabolism in F5 than PF/PFG during observed grasping (Raos et al, 2004, 2007), and increased prefrontal and reduced parietal activation compared to humans during the perception of actions and objects (Denys et al., 2004). Thus, the macaque and chimpanzee patterns of activation likely represent the ancestral primate condition. In contrast, humans' increased parietal and occipitotemporal activations during action observation are echoed by meta-analyses of over 100 fMRI and PET studies (Caspers et al., 2010; Molenberghs et al., 2009). This appears to represent greater functional investment in bottom-up perceptual representations incorporating greater kinematic and spatiotemporal details about the internal components of observed actions (Hecht et al., 2013). Accurate representation of these kinematic and spatiotemporal details is likely essential for flexible integration between individual learning and social acquisition of complex action sequences.

White matter circuitry has also undergone further adaptation after the chimpanzee-human divergence. The third branch of the superior longitudinal fasciculus (SLFIII), which links anterior inferior parietal cortex with ventral premotor cortex in monkeys, extends into more anterior regions of the inferior frontal gyrus in humans, particularly in the right hemisphere (Hecht et al., 2015). Notably, in macaques, SLFIII's projections from area PF terminate in ventral premotor cortex and do not reach prefrontal cortex (Petrides & Pandya, 2002, 2009). While chimpanzee SLFIII does show an observable extension into ventrolateral prefrontal cortex, connections with premotor cortex are far stronger, and SLFIII is not right-lateralized at the population level (Hecht et al., 2015). Ventrolateral prefrontal cortex, where SLFIII makes its anterior termination, is activated during tasks that require cognitive control, task switching, recursion, and sequencing, functions that are likely essential for the evolution of complex, hierarchically-structured instrumental behavior, including language. Notably, language is typically left-lateralized in the brain. We found anterior extension of human SLFIII in both hemispheres, but it was most marked in the right hemisphere; this asymmetry and its potential relationship to the lateralization of language is an issue that needs additional research.

Interestingly, in chimpanzees, prefrontal extension of right SLFIII is also associated with visual self-recognition. Not all chimpanzees can recognize their own reflection in a mirror, and there is a visible extension in the anterior aspect of right SLFIII projections from chimpanzees who do not recognize themselves in a mirror, to those who show ambiguous behavioral evidence, to those that clearly do (Hecht et al., 2015). Moreover, this same feature – right SLFIII's projection into anterior inferior frontal gyrus – shows structural change during the acquisition of Paleolithic stone tool use skills in modem humans trained to make these tools (Hecht et al., 2015), and the gray matter that is reached by this projection is activated by Acheulean, but not Oldowan, toolmaking (Hecht et al., 2015; Stout et al., 2011; Stout et al., 2008). Together, these results strongly implicate the extension of SLFIII white matter into right anterior inferior frontal gyms in the emergence of human-like visuomotor perceptual integration and action.

Thus, to summarize, comparative evidence on primate brain evolution points toward repeated waves of adaptation to the fronto-temporal-parietal action-perception circuitry. The ancestral primate state included early adaptations for visuomotor integration; apes evolved additional adaptations to the dorsal visual stream, likely related to the elaboration of behavioral capacities for imitation and manual gesture; and finally, this trend continued after humans diverged from other apes, with our ancestors evolving further perceptual sensitivities and white matter connections related to integration of bottom-up perceptual action details with higher-order, hierarchically-organized top-down cognitive processes including sequencing and recursion (Figure 1).



MODERN MACAQUES

Action observation circuitry heavily skewed toward ventral visual stream ("what" processing); Broca's area homolog has no direct connections with parietal area PF {involved in somatomotor processing for hand and mouth)

Functional brain responses to observed action are more prefrontally-focused than in humans; mirror system largely driven by object goals, with little or no response to observed intransitive action

MODERN CHIMPS

Action observation circuitry shows elaboration of the dorsal visual stream ("how" processing); prefrontal extension of SLFIII brings in put from PF into Broca's area homolog

Functional brain responses to observed action occur mainly in prefrontal cortex; mirror responses to intransitive action are very similar to mirror responses to transitive action

MODERN HUMANS

Action observation circuitry shows further elaboration of dorsal visual stream ("how" processing); further prefrontal extension of SLFIII into Broca's area, especially in the right hemisphere

Functional brain responses to observed action include substantial activation in occipitotemporal, parietal, and pre motor cortex, in addition to prefrontal cortex; mirror responses to intransitive action are very similar to mirror responses to transitive action

Figure 1. Schematic diagram of differences between extant primate species in the structure and function of brain circuitry for observing and producing action, and hypothesized selective forces in our shared evolutionary history

The chicken or the egg: Continuity, divergence, and the environmental context for change in brain-behavior evolution

The evolution of these circuits likely represents a cyclic interchange between selection pressures and neural changes, where existing neural features became exapted for new functions, which then supported the further exaptation of this circuitry for additional new functions. The chicken must predate the egg in brain-behavior evolution – newly adaptive behavioral and cognitive abilities can't emerge without the pre-existence of a neural architecture that can support them. But given that we are considering the evolution of *new* abilities, this neural architecture must have been previously supporting some other perhaps related function. What evolutionary mechanism mediated the exaptation of pre-existing neural adaptations for new functions? We argue that the emergence of new, complex, socially-learned behaviors on an evolutionary timescale is closely tied to adaptations for increased learning and neural plasticity on the timescale of an individual lifespan, an old idea (e.g, Bogin, 1997) which has recently gained a body of new experimental neuroscientific support, discussed below.

Flexibility and environmental sensitivity

A framework for the evolution of increased neural mechanisms for learning and plasticity is offered by Buckner and Krienen's "tethering hypothesis" (Buckner & Krienen, 2013). According to this model, in early mammals, whose cortex mainly consisted of primary sensory and motor regions, chemical signaling gradients constrained cortical networks to a rigid, canonical organization. In contrast, in human' evolutionary history, massive expansion of the cortical mantle "untethered" large regions from the constraints of signaling gradients, resulting in the emergence of distributed association networks with more flexible and plastic patterns of long-range connectivity.

We argue that these distributed, plastic association networks underlie a set of intertwined capacities that together have enabled human technological culture to evolve so rapidly: our ability to socially transmit, and incrementally improve upon, learned behavioral skills; our use of language and other forms of symbolic representation; and our proficiency for tool use and tool-making. These capacities all involve similar (but non-identical), overlapping networks in lateral frontal, temporal, and parietal cortex (reviewed in (Stout & Chaminade, 2012)), and we and many other researchers have considered it likely that some or all of these functions coevolved (e.g., (Arbib, 2012; Fitch et al., 2010; Greenfield, 1991; Hopkins et al., 2007; Pulvermuller & Fadiga, 2010; van Schaik et al., 1999)). In particular, studies by our group and other collaborators have found multiple lines of evidence suggesting human adaptation in these networks.

Some additional compelling recent data is consistent with this idea. Gomez-Robles et al. (2015) compared the heritability of cortical morphology in chimpanzees and humans that had known kinship relationships. Morphology was less heritable in humans, and notably, this effect was most pronounced in association areas. Buckner et al. (2013) have produced a map of individual variability in human functional connectivity, which reflects patterns of co-activation between various brain regions; again, this is greatest in association regions. It seems likely that individual differences in actual anatomical connectivity could underlie this functional and morphological variation, and indeed Gomez-Robles et al. (2013, 2015) postulate that their results may be related to underlying changes in neural circuitry. Additional support for the tethering hypothesis can be found in the high degree of individual variation in human brain organization. This contrasts with the brains of most other vertebrate species, which are quite similar across individuals, especially in primary cortical regions and in subcortical regions involved in the production of species-specific behaviors (e.g., Finlay et al., 2011). In humans, considerable individual neuroanatomical variability occurs in our species' greatly expanded association cortex. For example, humans show high individual variation in the location, extent, and internal organization of classical language regions (Anwander et al., 2007; Galaburda et al., 1991), and in the gray matter density, topography, and functional organization of posterior parietal association regions (Frey et al., 2005; Kanai et al., 2011; Ryan et al., 2006). The extent of individual variability in association regions appears to be greater in humans than in chimpanzees, as indicated by a recent comparative study on cortical morphology (Gomez-Robles et al., 2014).

Specificity and innateness

There is a key evolutionary implication of this relaxed genetic constraint: given that human brain organization has become less pre-ordained by developmental programs, it may therefore be more responsive to the input of individuals' experiences with the physical, social, and cultural environment, providing a physiological mechanism for plasticity underlying the acquisition of learned skills.

Selection for increased plasticity may have occurred because it maximizes the impact of learning on shaping these circuits. Consistent with this idea, human neocortex is characterized by a prolonged myelination period (Miller et al., 2012). During human development, association regions expand nearly twice as much as other regions (Hill et al., 2010) and also myelinate impressively late – into the second and third decade of life (Buckner & Krienen, 2013; Flechsig, 1920; Yakovlev & Lecours, 1966). Interestingly, comparisons with macaques suggest that this pattern of developmental expansion is mirrored by the pattern of evolutionary expansion, perhaps because it is adaptive for recently-evolved regions to mature more slowly, to increase the influence of early experience on those regions (Hill et al., 2010). Together, these results point toward a role for increased plasticity in human brain evolution, allowing for increased flexibility and sensitivity to environmental input in the acquisition of learned behaviors like language.

Situated in opposition to this idea of reduced innateness in human brain organization, is the idea that given constant environmental selection pressure, over time, behaviors that are tightly tied to survival will tend to become earlier-developing and more-automatic, with increasingly reliable and invariable emergence in every individual. Mutations that lead the learned behavior to be easier or faster to acquire will tend to be favored. This phenomenon is termed the Baldwin Effect (Baldwin, 1896; Osborn, 1896; Weber & Depew, 2003; Bateson, 2004). It describes a mechanism by which pre-existing brain anatomy can become coopted for learned skills – i.e., by which learned behaviors can become (at least somewhat) innate. Importantly, the Baldwin Effect can only occur if the environment favoring the learned behaviors is relatively constant; socially-transmitted culture can provide some aspects of environmental stability while also providing a mechanism for continued change. Thus, the Baldwin Effect describes a process by which biological evolution can co-occur with, and be driven by, cultural evolution; we and others have proposed that the Baldwin effect played a role in the evolution of neural circuits for learned, socially-transmitted skills, including language and complex tool use (Hecht et al., 2015).

Clearly, though, language is not entirely "innate;" i.e., it does not emerge without the requisite environmental input and experience. Thus, a mechanistic explanation for the evolution of language must go beyond identifying the circuits that have changed and address the inherent trade-off between the evolutionary pressure for underlying neural systems to be flexible and sensitive to environmental input vs. the tendency for adaptive behaviors to become more innate over time. On an evolutionary timescale, how are these opposing forces balanced, and what are the selective contexts that tip the balance toward one or the other? And on a mechanistic level, how are these changes mediated? We propose that these are important questions for future research on language evolution.

Toward a new road map

In conclusion, the comparative research reviewed here points toward some key transitions relevant to the evolution of what eventually became language circuitry. In general, the ideas outlined here agree with the MSH in the hypothesis that waves successive adaptations to frontoparietal vision-for-action and action-perception circuitry were crucial for the evolution of language. The current evidence points toward (1) the elaboration of the dorsal visual stream, including the emergence of new areas, new functional sensitivities, and increasing elaboration of white matter circuitry; (2) the elaboration and emergence of cognitive and behavioral capacities thought to be supported by the dorsal visual stream, and by integration of dorsal- and ventral-stream visual processing with hierarchical representations; and (3) an increase in plasticity in human association circuits, facilitating the learned acquisition of socially transmitted skills, including tool use, gesture, and language. Important targets for future research include mechanisms mediating the tradeoff between evolutionary trends toward increasing innateness and increasing plasticity, and the physiological and anatomical mechanisms which linked this evolving vision-for-manual-action circuitry with vocal and auditory circuitry in spoken language.

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