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A model for Social Communication And Language Evolution and Development (SCALED)

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In humans, brain connectivity implements a system for language and communication that spans from basic pre-linguistic social abilities shared with non-human primates to syntactic and pragmatic functions particular to our species. The arcuate fasciculus is a central connection in this architecture, linking regions devoted to formal aspects of language with regions involved in intentional and social communication. Here, we outline a new anatomical model of communication that incorporates previous neurofunctional accounts of language with recent advances in tractography and neuropragmatics. The model consists of five levels, from the representation of informative actions and communicative intentions, to lexical/semantic processing, syntactic analysis, and pragmatic integration. The structure of the model is hierarchical in relation to developmental and evolutionary trajectories and it may help interpreting clinico–anatomical correlation in communication disorders.

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Introduction

Classical neurological models of language consist of the arcuate fasciculus connecting Broca's and Wernicke's regions dedicated to speech production and comprehension, respectively. This dorsal network is considered pivotal in syntactic analysis and auditory–motor transcoding. In addition to classical language areas, several studies have suggested that the anterior temporal lobe is crucial for lexical and semantic processing. Hence, the majority of language models are based on a dual stream, a dorsal phonological route for mapping sound into words and a ventral semantic route for mapping sound into meaning [1–3].

The dual stream model may represent an oversimplification as recent evidence based on tractography suggests that language relies on a more extended network encompassing additional connections to the inferior parietal lobule [4,5] and the dorsomedial frontal cortex [6,7•]. These connections seem to underlie other aspects of communication, at the interface between language and social cognition, in the domain of pragmatics [8,9,10•,11••].

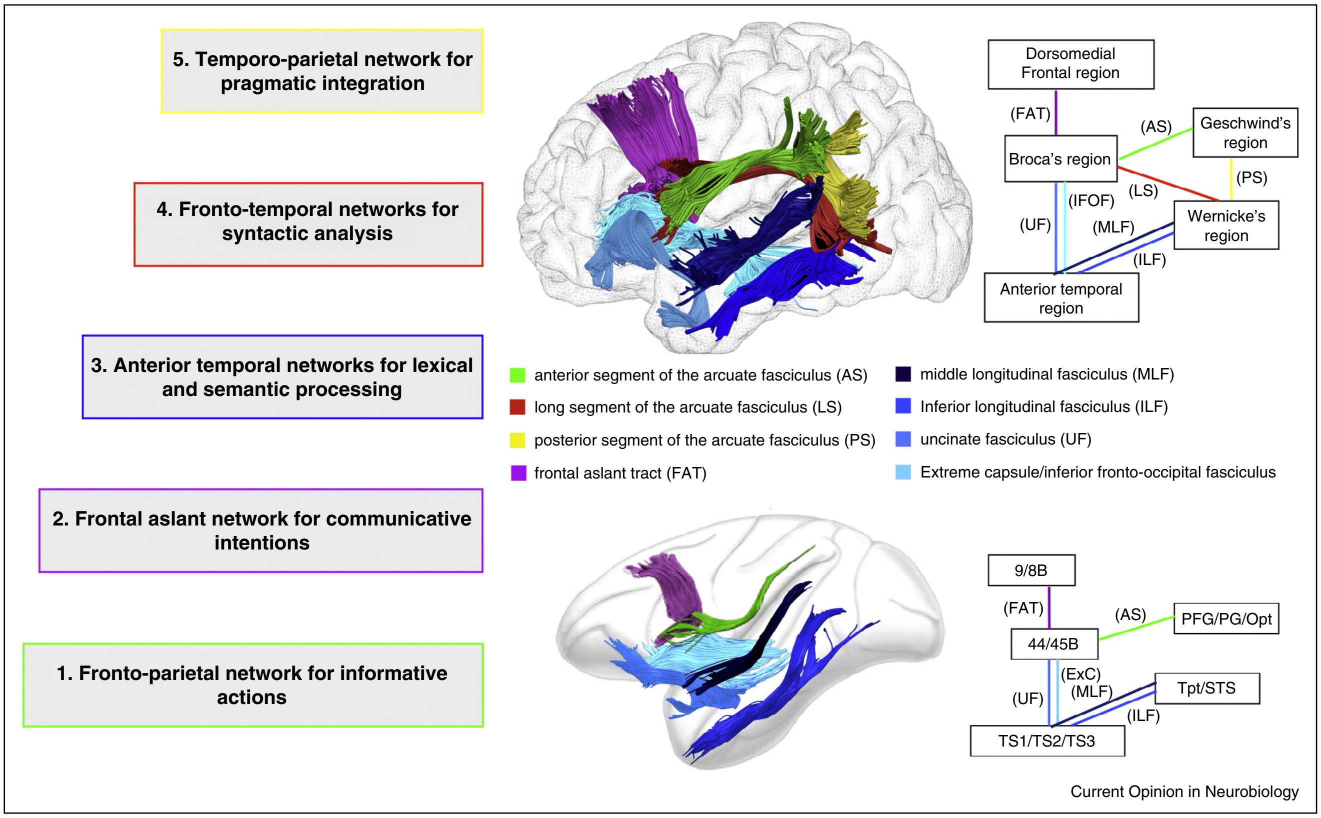
In this article we review and integrate these recent developments in a five-tiered anatomical model of social communication and language (Figure 1). The model includes different aspects of language knowledge and use, from basic recognition of pre-linguistic informative actions to complex pragmatic interpretation. The model is primarily based on imaging studies in humans and finds support from developmental studies, comparative anatomy, and observation of animal behaviour. A key feature of the model is the hierarchical organization of the five levels according to developmental and evolutionary aspects of social communication.

Level 1. A fronto-parietal network for informative actions

Within the arcuate fasciculus, a subset of fibres (anterior segment) links Broca's region to Geschwind's region in the inferior parietal lobule (Figure 1, green colour) [4]. This fronto-parietal network connects the so-called mirror neurons that activate not only during motor execution, but also when observing movements performed by others. By mapping the sensory representation of actions and sounds made by others onto internal motor representations, the mirror neuron network may implement a cognitive mechanism of action understanding [12]. In this view, the mimetic abilities embodied in mirror neurons provide a first step towards social development and engagement, a necessary perceptual bridge in which the observer recognizes in the observed agent his own ability to produce the same actions.

This network acts as an attentional bottleneck through which perceived visual and auditory stimuli become relevant information [13] that is prioritized for further use in social behaviours. In the context of communication, the intersubjective resonance supported by the fronto-parietal mirror network may permit the recognition of another individual as an agent capable of conveying

Figure 1



A model for Social Communication And Language Evolution and Development (SCALED). On the left, the boxes contain the major networks and their corresponding functions for language and social communication in a hierarchical scale, reflecting developmental and evolutionary trajectories. The colours of the boxes correspond to the tractography reconstruction of the tracts indicated in the centre, for the human (upper panel) and macaque monkey brain (lower panel). On the right, the diagrams show the brain regions connected by each network. Brain regions are defined as follows: Broca's area includes part of the precentral gyrus and the posterior cortex of the inferior and middle frontal gyrus; Wernicke's region extends over the posterior cortex of the superior and middle temporal gyrus; Geschwind's region corresponds to the inferior parietal lobule, including supramarginal and angular gyrus; the dorsomedial frontal cortex includes anterior SMA, preSMA and medial prefrontal cortex; the anterior temporal region encompasses the superior, middle and inferior temporal cortex anterior to Wernicke's region, and the temporal pole. The putative equivalent regions in the macaque brain are also indicated in the lower diagram. Level 1: in humans, the anterior segment of the arcuate fasciculus (AS; green) connects posterior cortex of Broca's region to anterior cortex of Geschwind's region (supramarginal gyrus). This fronto-parietal network implements a system for recognition and production of informative actions. In the macaque monkey brain this tract corresponds to the third branch of the superior longitudinal fasciculus (SLF III). Level 2: the frontal aslant tract (FAT; purple) connects Broca's region to the dorsomedial frontal cortex, forming a frontal aslant network for the processing communicative intentions. This tract is present in the macaque monkey brain. Level 3: the ventral network for lexical and semantic processing is composed of several tracts. The middle longitudinal fasciculus (MLF; dark blue) and inferior longitudinal fasciculus (ILF; like blue) connect Wernicke's region to the anterior temporal region, whereas the uncinate fasciculus (UF; azure) connects the anterior temporal region to Broca's region. Some fibres of the inferior fronto-occipital fasciculus (IFOF; cyan) (corresponding to extreme capsule in monkey anatomy; ExC) connect posterior temporal regions (including perhaps Wernicke's region in humans) to the frontal lobe. Significant differences exist between the human and macaque brain in the anatomy of these ventral pathways (e.g. in the monkey brain the ILF connects occipital to temporal region, due to the absence of the middle temporal gyrus). Level 4: the long segment of the arcuate fasciculus (LS; red) connects Broca's and Wernicke's region, supporting a fronto-temporal network for syntactic analysis and other functions. In the monkey the portion of the long segment projecting to the middle temporal lobe is absent. Level 5: the posterior segment of the arcuate fasciculus (PS; yellow) links Wernicke's region to Geschwind's region (primarily to the angular gyrus), forming a temporo-parietal network for pragmatic integration at the highest level of communication (level 5). In the monkey brain the connections between posterior temporal and angular gyrus are poorly developed.

relevant information (i.e. as an informative agent). At the same time, the fronto-parietal network may support the sensory-motor integration necessary to produce actions relevant for others (i.e. informative actions).

The areas connected by the fronto-parietal network myelinate early during development and a simian–human equivalence of these connections has been well documented [14••]. Consistently, sensory-motor mapping seems to develop very early in newborns [15]. Older infants are able to direct special attention to humans as opposed to objects and use available information for further elaboration [16]. This probably reflects the pre-communicative stage in language development, when children identify another agent as a relevant source of information, but are still unable to express and recognize communicative intentions. The third branch of the superior longitudinal fasciculus (SLF III) in the monkey brain corresponds to the anterior segment of the arcuate fasciculus in the human brain. Indeed, neurons in monkey's posterior parietal cortex are sensitive to the interaction between agents [17], suggesting a common anatomical basis for the recognition of informative actions across species. This ability is the first step in the process of engaging in social interaction and a fundamental precursor of recognition and expression of communicative intentions.

Level 2. A frontal aslant network for communicative intentions

Broca's region is also connected to the dorsomedial frontal cortex via a newly described fascicle we termed the 'frontal aslant tract' (Figure 1, purple colour) [6,18,19]. A number of studies identified the posterior portions of the dorsomedial frontal cortex (pre-supplementary motor area) as involved in distinguishing self from others' actions [20], action monitoring [21] and low-level aspects of mentalizing [22]. More anterior areas (the medial prefrontal cortex) are involved in higher aspects of mentalizing, being implicated in the representation of our own as well as other's mental states [23]. This representational capacity permits the receiver to grasp what the 'sender' intends the interlocutor to understand, closing the loop between interacting minds [24••]. The frontal aslant network may thus constitute the neural underpinning of the expression and recognition of communicative intentions. Compared to the fronto-parietal network of the level 1, which engages in sensory-motor aspects of social interaction, the frontal aslant network may process more cognitive and inferential aspects of communication.

In this view, this second step in the evolution and development of communicative abilities permits the observer to recognize that the informative agent has also an intention to convey a message (i.e. he is an intentional agent) and to engage in a communicative exchange. This is an adaptive aspect of the communicative process that lies at the core of pragmatic accounts of communication [13,25], from basic mechanisms of gestural expression and emotion recognition to vocalization and verbal interaction.

The early maturation of the frontal aslant tract [26] and findings from comparative biology [14••] might help explaining a range of basic communicative behaviours observed in infants and great apes. The mere presence of an agent automatically triggers processes of belief attribution related to 'social sense' in toddlers as young as seven months [27]. Infants are also are able to express pragmatic functions like requesting or asserting through pointing even before developing language [28]. Later in life, when expression becomes primarily verbal, the connections between the dorsomedial frontal cortex and Broca's region allow for conveying communicative intentions through speech. The frontal aslant tract is developed also in macaque monkeys [14••], and one may hypothesize its existence in great apes as well, consistently with their capability of employing intentional communication, mainly imperative gestures aimed at attracting attention or at initiating an action [29]. An interesting observation is that in humans, as opposed to macaque monkeys, the frontal aslant tract seems to extend to more anterior areas that are involved in theory of mind processes, [30]. The more anterior connections of the frontal aslant tract may underlie the ability to infer abstract meanings based on sophisticated mentalizing abilities in humans. Overall, this frontal aslant network may provide the basis for intentional communicative acts in humans and to some extent non-human primates. Nevertheless, this network is limited in conveying more elaborated meanings based on a well-developed system for lexical and semantic processes.

Level 3. Anterior temporal networks for lexical and semantic processing

Wernicke's region is connected to the anterior temporal lobe via the middle and inferior longitudinal fasciculus (Figure 1, dark and light blue colours, respectively). Furthermore, connections from the anterior temporal lobe to anterior Broca's region run through the uncinate fasciculus (Figure 1, azure colour) [7•,31,32]. In addition, other authors describe direct connections between Wernicke's and Broca's region through the inferior fronto-occipital fasciculus (Figure 1, cyan colour) [2].

These ventral networks have been extensively described as involved in lexical and semantic processing at different levels. The superior temporal gyrus has a key role in speech recognition, while the middle and inferior temporal gyri are pivotal in accessing lexical and semantic representations from the acoustic inputs [1,33]. Along the middle and the inferior longitudinal fasciculus the temporal cortex is involved in selecting verbal labels for objects in a posterior–anterior progression of word comprehension, from generic to specific levels of precision [34••]. Overall, the anterior temporal networks enable mapping sound into meaning, allowing for various phonological, lexical and semantic operations. In addition, by projecting into frontal areas through the uncinate fasciculus, this route translates lexical representations into articulatory representations [35••].

Ontogenetically, this ventral route appears to develop very early [36••] and may correspond to the observed behaviour of children, where word production starts around 12 months and accelerates at around 18 months.

This vocabulary spurt probably marks the transition from simple vocalization routines to the referential use of words, when children gain the 'naming insight' and learn to pair sounds to objects. There is evidence that the ventral route also exists in macaque monkeys [14••,37], but is less developed, as they lack the middle temporal gyrus and their inferior longitudinal fasciculus connects primarily to posterior occipital areas. This might match the lexical and semantic abilities of primates, which are able to use signs when referring to representation [38]; nevertheless the size of their vocabulary is limited, and a vocabulary spurt has never been reported. The gap between human and non-human abilities becomes even more prominent when it comes to combinatorial abilities related to syntax.

Level 4. A fronto-temporal network for syntactic analysis

The long segment of the arcuate fasciculus connects directly Broca's and Wernicke's regions (Figure 1, red colour) [4,39•]. A significant portion of this dorsal network (especially projections to the middle temporal gyrus) is involved in syntactic production and comprehension. Broca's region activates in tasks involving processing of syntactically complex sentences and acquisition of grammatical rules [40••,41•] while the middle temporal gyrus in Wernicke's region participates in syntactic analysis [42].

Successful syntactic processing requires the interplay between lexical properties and syntactic analysis, which is mediated by the joint activation of the whole fronto-temporal system connected through the long segment of the arcuate fasciculus [42]. The long segment seems thus to be of particular importance for higher-order language functioning, especially at the syntactic level. Other fibres of the long segment (especially those originating from the superior temporal gyrus) are fundamental in other tasks requiring auditory–motor interaction [35••], such as word repetition [4] and word learning [43].

One important consideration concerns the late development of the long segment of the arcuate fasciculus. The immature status of this connection in children under the age of 7 has been related to the inability to understand complex aspects of syntax [36••]. In the macaque monkey the long segment originates only from a small posterior portion of the superior temporal gyrus and is much smaller than in humans, where it departs from the superior, middle and perhaps part of the inferior temporal gyrus [14••,44]. This is consistent with the limited combinatorial abilities of non-human primates [45]. The development of the most posterior fibres of the long segment of the arcuate fasciculus for syntactic competence thus represents a leap forward in the evolution of human language. Humans, however, have reached a further level of complexity in their use of language in social context through the highly flexible manipulation of symbols and meanings based on sophisticated pragmatic abilities.

Level 5. A temporo-parietal network for pragmatic integration

The posterior segment of the arcuate fasciculus is a short vertical tract connecting Wernicke's region to the Geschwind's region (especially the angular gyrus) (Figure 1, yellow colour) [4,39•]. This temporo-parietal network is involved in semantic aspects of language processing [46] and high-level social cognition [22,23,24••]. This connection has also a key role in stimulus-driven control of attention and diverting self-reflective thinking to salient external stimuli [47]. In addition, the temporo-parietal network is a hub for multi-sensory integration, in particular visual–auditory, necessary for semantic and contextual interpretation of language and communicative actions. This network is, therefore, well placed for deriving the speakers' meaning at the highest level of communication.

In neuropragmatics studies the angular and posterior temporal cortices activate in tasks for the comprehension of metaphors and figurative language [48], indirect speech acts [49], as well as for the representation of discourse [50] and the protagonist's perspective in narratives [51]. This evidence suggests that in communication the temporo-parietal network supports complex integration and inferential mechanisms, well beyond the simple recognition of communicative intentions in level 2 [10•,11••]. These mechanisms may reach several layers of meta-representations for the attribution of beliefs and emotional states to conversational partners [52].

Behavioural evidence suggests that full-fledged pragmatic abilities are attained late in development, and some aspects of figurative language comprehension, for example, the ability to grasp ironic meanings, gradually evolve throughout late childhood [53]. This is in line with anatomical studies showing that the angular gyrus is one of the latest region to myelinate in the human brain. In addition, compared to the other segments of the arcuate fasciculus, the maturational changes in the temporo-parietal connections continue throughout adolescence [54]. By contrast, there is little evidence that other species can take into account other's intentional or mental states in order to adjust their communicative formulation [29]. Non-human primates, while being able to express communicative gestures operating on the recognition of the other's actions (level 2), do not show the same degree of flexibility of humans and cannot reach the complexity of symbolic manipulation as in figurative and indirect speech. The poor development of the posterior segment of the arcuate fasciculus in the monkey brains [54] suggests that this network could underlie uniquely human abilities, although better data from apes are needed to support this suggestion (see Rilling, in this issue).

General features of the model

In this paper we reviewed the recent literature on language networks, in particular evidence of a dorsal and a ventral stream, and we incorporated newly described connections involving the inferior parietal lobule and the dorsomedial frontal cortex. Our proposal consists of a hierarchical neuroanatomical model that integrates aspects of language and social cognition for communication. Each level of the model lays out the ground for the acquisition of higher social, linguistic and pragmatic competence, reflecting developmental and possibly evolutionary aspects of communicative behaviour.

Previous works suggest that levels 1 and 2 are attained within the first year of life, levels 3 and 4 are acquired later, and level 5 fully develops only in late childhood and adolescence. Furthermore, preliminary comparative anatomical studies indicate that, while networks underlying level 1, and in part 2 and 3, are shared between humans and non-human primates, levels 4 and 5 rely on networks uniquely well-developed in humans.

The model also entails shared neural representations for production and comprehension at each level. This organization is supported by studies showing an overlap of activation for non-verbal tasks involving generating and understanding communicative intentions [55], as well as producing and comprehending semantic and syntactic aspects of the sentence [56].

Studies in neurodevelopmental disorders support the hierarchical features of the model. In autism spectrum condition and schizophrenia, for example, social and language abilities are affected at different levels. Children with low functioning autism show impaired recognition of action and communicative intention (levels 1 and 2 of our model). These children also fail to develop normal language (levels 3 and 4) and pragmatic competence (level 5) [57]. On the other extreme of the spectrum, individuals with Asperger's syndrome show no language delay but they are impaired at the pragmatic level, in tasks involving understanding context-dependent expressions, such as irony [58]. Recent tractography studies on autism spectrum condition show altered white matter connections in several tracts of the networks implicated in our model possibly reflecting social and language impairments at different levels [59,60]. Of particular relevance for the stepwise acquisition implied by our model is the condition known as childhood disintegration disorder [61], where children develop a normal language up to level 3 and partly 4, after which they reverse to early stages of development and show autistic features. In patients with schizophrenia, a disorder with onset in late adolescence and early adulthood, impairments in pragmatics and social cognition (level 5) are well documented [62], which could be related to reported abnormal anatomy of the posterior segment of the arcuate fasciculus [63].

Data from disorders affecting language and communication in older ages support the anatomical and functional distinction of the model. In patients with primary progressive aphasia, reduced verbal fluency in speech production correlates with damage to the frontal aslant tract [7•], with possible implications on the ability to initiate intentional communication (level 2). Moreover, in these patients semantic deficits correlate with abnormalities of the anterior temporal networks (uncinate fasciculus) (level 3) [34••], while syntactic deficits correlate with alteration of the long segment of the arcuate fasciculus (level 4) [64].

Limitations and future directions

We hope that the SCALED model will help to integrate anatomical and neurolinguistic approaches to communicative behaviour. Yet multiple features of the model remain to be clarified. A crucial difficulty for our proposal is its reliance on anatomical evidence derived primarily from axonal tracing in macaque monkeys and diffusion tractography in humans. Both methods have several advantages but their current limitations hinder our detailed knowledge of comparative anatomy [65]. Considering the inapplicability of axonal tracing methods to humans, the solution to this impasse will come from advances in diffusion imaging. Future developments in the field of tractography are likely to benefit from data acquired at higher spatial resolution [66] and advanced methods for reducing artefactual reconstructions [65]. These improvements will allow obtaining reliable information from a wider range of individuals across species, including exemplars for which there is currently little anatomical information (e.g. great apes).

Furthermore, the networks listed in our model present a great variability in their left/right lateralization, which may play a role in clinical symptom expression and functional recovery [39•]. Most of these networks are also involved in other cognitive functions (e.g. verbal working memory, emotional processing, attention) that participate to the normal development of social communication and language. The combination of advanced tractography methods with functional approaches and more ecologically valid paradigms will be key to validate the model and further define its components.

Conflict of interest statement

Nothing declared.

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