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BULLETIN N° 216
ACADÉMIE EUROPEENNE INTERDISCIPLINAIRE DES SCIENCES
INTERDISCIPLINARY EUROPEAN ACADEMY OF SCIENCES

Lundi 12 juin 2017:
à 17 h à la Maison de l'AX, 5 rue Descartes 75005 PARIS

Conférence de Luc STEELS, Professeur à l'Institut de Biologie évolutive (UPF-CSIC) de Barcelone/Espagne :
"***Comment pouvons nous développer des théories scientifiques relatives à l'origine et à l'évolution des langages***"

Notre Prochaine séance aura lieu le lundi 11 septembre 2017 à 17h
5 rue Descartes 75005 PARIS

Elle aura pour thème

I. Conférence du Pr Stanislas DEHAENE,
Membre de l'Institut (Académie des Sciences), Professeur au Collège de France
Directeur de l'unité de Neuro-Imagerie Cognitive, INSERM-CEA-Université Paris Sud
Directeur du centre NeuroSpin
"***Progrès récents dans la Compréhension de la Conscience et de ses Désordres***"

II. Eventuel Examen de Candidature(s)

Académie Européenne Interdisciplinaire des Sciences
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ACADÉMIE EUROPÉENNE INTERDISCIPLINAIRE DES SCIENCES
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Conférence du Pr Stanislas DEHAENE,
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ACADEMIE EUROPEENNE INTERDISCIPLINAIRE DES SCIENCES
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5 rue Descartes 75005 PARIS

Séance du Lundi 12 juin 2017 /Maison de l'AX 17h

La séance est ouverte à 17h **sous la Présidence de Victor MASTRANGELO** et en la présence de nos Collègues Gilbert BELAUBRE, Jean-Louis BOBIN, Juan-Carlos CHACHQUES, Gilles COHEN-TANNOUDJI, Alain CORDIER , Jean-Felix DURASTANTI, Michel GONDRAN, Irène HERPE-LITWIN, Gérard LEVY, Pierre MARCHAIS, Claude MAURY, Jean-Jacques NIO, Marie-Françoise PASSINI, Edith PERRIER, Jean SCHMETS , Alain STAHL, Jean-Paul TEYSSANDIER , Jean-Pierre TREUIL, .

Etaient excusés :François BEGON, Jean-Pierre BESSIS, Bruno BLONDEL, Michel CABANAC, Alain CARDON, Daniel COURGEAU, Sylvie DERENNE, Ernesto DI MAURO, Françoise DUTHEIL, Claude ELBAZ, Vincent FLEURY, Robert FRANCK, Jean -Pierre FRANCOISE, Dominique LAMBERT, Valérie LEFEVRE-SEGUIN, Antoine LONG, Anastassios METAXAS, Alberto OLIVIERO, Pierre PESQUIES, Jacques PRINTZ, Michel SPIRO, Mohand TAZEROUT , Jean VERDETTI.

I. . Présentation de notre conférencier Luc STEELS par notre Président Victor MASTRANGELO:

Luc Steels a étudié la linguistique à l'Université d'Anvers (Belgique) et l'informatique au MIT (USA). L'Intelligence Artificielle (IA) comprenant une vaste gamme de capacités intelligentes incluant la vision, le comportement des robots est son principal domaine de recherche , les représentations conceptuelles et le langage, est son domaine principal de recherche. En 1983, il est devenu Professeur d'Informatique à l'Université libre de Bruxelles (VUB). Il a été le cofondateur et le président (de 1190 à 1995) du VUB Computer Science Department (Faculté des Sciences de Bruxelles) - laboratoire d'Intelligence Artificielle -.

Il a fondé le Sony Computer Science Laboratory in Paris (Laboratoire d'informatique de Sony à Paris) en 1996 dont il a été le premier directeur.

Actuellement il est Professeur Chercheur à l' ICREA (Institution Catalane pour la Recherche Avancée) à l'Institute for Evolutionary Biology de Barcelone (CSIC -Conseil pour la Recherche Scientifique Espagnole -,UPF - Université Pompeau Fabra -).

Steels a participé à une douzaine de projets européens à grande échelle et il a dirigé plus de 30 thèses d'état soutenues.

Il a produit plus 200 articles dans des revues à comité de lecture et édité 15 livres en relation directe avec sa recherche. Durant les 10 dernières années il s'est axé sur les théories concernant les origines et l'évolution du langage en utilisant des simulations informatiques et des expériences robotiques pour les découvrir et les tester.

Parmi les publications notre Président mentionne les plus récentes::

- Beuls, K., & Steels, L.. (2013). Agent-Based Models of Strategies for the Emergence and Evolution of Grammatical Agreement. *PLoS ONE*, *8*(3), e58960. doi:10.1371/journal.pone.0058960

- Wellens, P., van Trijp, R., Steels, L., & Beuls, K.. (2013). Fluid Construction Grammar for Historical and Evolutionary Linguistics. *Proceedings of the 51st Annual Meeting of the Association for Computational Linguistics*. presented at the 08/2013, Sofia, Bulgary.
- Steels, L. (2011). Modeling the cultural evolution of language. *Physics of Life Reviews*, *8*, 339 - 356. doi:10.1016/j.plrev.2011.10.014

Il a donné une émission en 2013 sur Radio-France sur les sources de la parole.

Il a également été "reviewer" (examinateur) dans diverses revues scientifiques: Nature, Cognitive Science, Artificial Life, Artificial Intelligence, Cognition, Robotics and Autonomous Systems.

Il a été membre de jurys de thèse à Montpellier , à Paris , Bruxelles , Grenoble, à l'ENS de Paris , Hambourg, Barcelone, Amsterdam.

Il exerce un rôle dans divers organismes scientifiques:

- Membre de la New York Academy of Sciences
- Membre fondateur du conseil de ECCAI, l'organisation européenne pour l'Intelligence artificielle . A contribué à l'établissememnt du siège d' ECCAI, en Belgique
- Membre du comité de direction de la " Society for AI (*IA en français*) and Simulation of Behavior"(jusqu'en 1990).
- Président fondateur (de 1984 à 1994) de l'association belge pour l'IA , qui a depuis fusionné avec l'organisation néerlandaise sur l'IA devenant le BNVKI.
- Membre du comité consultatif scientifique du GMD, l'Institut National Allemand de Recherche en Informatique de 1996 à 2000 lorsque GMD est devenu membre de Fraunhofer Institut.
- Membre du comité consultatif scientifique de DFKI, le Centre National Allemand de Recherche en Intelligence Artificielle (de 1988 à 1993)
- Membre du comité consultatif scientifique de Board Electrum (Institut National Suédois en Informatique) (en 1994)
- Membre de la commission FWO pour l'informatique
- Membre de l'Académie Royale Flamande de Belgique des Sciences et des Arts

Il est co-éditeur et co-fondateur de: journaux :

- (avec Bob Wielinga) jusqu'au début des années 90 de: AI Communications (devenu la principale revue européenne en IA)
- (avec Sherman Wilcox)) de Journal Evolution of Communication. (Walter Benjamins)

Il est éditeur associé de :

- Artificial Life Journal (MIT Press)
- Adaptive Behavior Journal (Sage Publications, London)
- Journal of Universal Computer Science (Springer)
- Journal of Complex Systems (Hermes)
- Journal of Genetic Programming and Evolvable Machines (Kluwer)

Il est membre du comité de rédaction de

- Cognitive Science Quarterly (Hermes)
- In Cognito (Grenoble) (French)
- Artificial Intelligence Abstracts (until 1991)

Parmi les livres publiés notre Président cite les trois derniers:

- **Computational Issues in Fluid Construction Grammar** Springer Verlag 2012
- **Language Grounding in Robots** L. Steels and M. Hild (Eds) Springer Verlag, 2012
- **Design Patterns in Fluid Construction Grammar** L. Steels (Ed) John Benjamins Publishing Company, 2011

Le Pr Luc STEELS est également l'auteur de plusieurs pièces de théâtre et livrets d'opéra ayant fait l'objet de représentation dans des établissements très reconnus internationalement. (Avignon, Chaillot, Palais de la Musique de Barcelone etc ...).

Pour toute information complémentaire on peut aller sur le site : https://ai.vub.ac.be/members/steels

II. Conférence du Pr Luc STEELS

Résumé de la conférence: "Comment peut-on développer des théories scientifiques pour l'origine et l'évolution des langages? "

Le problème de l'évolution des langages continue de susciter l'intérêt de nombreuses disciplines scientifiques. Clairement, il existe une composante biologique responsable car le langage met en jeu d'extraordinaires capacités cérébrales. Il existe également une composante sociale puisque le langage n'a de sens que dans des communautés dont les membres doivent intensément coopérer pour survivre et élever leurs enfants. Ici je vais me concentrer sur la troisième composante , tout aussi importante, la composante culturelle: quels sont les schémas d'interactions et les fonctions cognitives grâce auxquels une communauté peut organiser elle-même un système linguistique avec des propriétés analogues à celles que nous trouvons dans les langages humains.

Je me suis attaqué à cette approche avec mon groupe à l'aide d'expériences comportant des agents artificiels (si possible incorporés dans des robots humanoïdes) qui actionnent des jeux de langage. Cette approche expérimentale nous permet de poser des questions extrêmement précises, telles que *comment et pourquoi* la structure grammaticale de la phrase apparaît, ou *comment et pourquoi* un type de système émerge et s'effondre et de mettre à l'épreuve des théories susceptibles de répondre à ces questions. La conférence ne discutera pas seulement des exemples concrets de cette approche mais elle s'efforcera d'extraire la théorie générale de l'évolution des langages issue de ce travail.

Annonces

I. **Quelques ouvrages papiers relatifs au colloque de 2014 " Systèmes stellaires et planétaires- Conditions d'apparition de la Vie"   -**

- Prix de l'ouvrage :25€ .
- Pour toute commande s'adresser à :

Irène HERPE-LITWIN Secrétaire générale AEIS
39 rue Michel Ange 75016 PARIS
06 07 73 69 75
irene.herpe@science-inter.com

Documents

Pour compléter l'intervention du Pr Luc STEELS nous vous proposons:

p.08 Un article du Pr Luc STEELS intitulé "Do *Languages evolve or merely change*?" publié sur le site https://www.researchgate.net/journal/0911-6044_Journal_of_Neurolinguistics de novembre 2016.

Pour préparer l'intervention du Pr Stanislas DEHAENE nous vous proposons :

p. 18 un article des Pr Stanislas DEHAENE et Jean Pierre CHANGEUX intitulé "*Experimental and Theoretical Approaches to Conscious Processsing"* publié dans Neuron 70, April 28, 2011 ª2011 Elsevier Inc..accessible sur le site https://www.ncbi.nlm.nih.gov/pubmed/21521609.

Do languages evolve or merely change?

Luc Steels
ICREA, Institute for Evolutionary Biology (UPF-CSIC),
PRBB, Dr. Aiguadar 88, 08003 Barcelona, Spain

Abstract

The paper clarifies the point of view of evolutionary linguistics, a field that seeks causal explanations for language change as observed by historical linguists by using theoretical models gleaned from contemporary evolutionary biology, in particular replicator-dynamics and level formation.

1. Introduction

In a recent publication, Berwick and Chomsky state: "Languages change, but they do not evolve. It is unhelpful to suggest that languages have evolved by biological and nonbiological evolution - James Hurford's term. The latter is not evolution at all." [1], p. 52. This view is actually quite common in linguistics, but there is a growing group of 'evolutionary linguists' who believe, on the contrary, that an evolutionary perspective is not only appropriate but our best bet for understanding language evolution ([6], [7], [17], [13], [2], [19], a.o.). The objective of this paper is to explicate better this position and thus overcome an unproductive dichotomy and fruitless debate.

Clearly the question of language origins decomposes into two: (1) the evolution of the language faculty and (2) the evolution of languages (Spanish, Italian, Japanese, Indonesian, etc.).

(1) The language faculty is the set of neurobiological mechanisms needed for processing and learning language. Research about the nature and origins of the language faculty today often goes under the banner of *biolinguistics* [5]. It must obviously rest on adequate models of language processing and learning (as developed in psycholinguistics and computational linguistics), and their implementation in neural processing (as researched in neurolinguistics). Once we have a clear idea about the biological basis of language, which is certainly not the case today, the incredibly powerful machinery of evolutionary biology is available to

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investigate the genetic basis of the relevant brain structures, how and when the implicated genes could have appeared in the human lineage, what kind of selectionist pressures were operating, how the genes steer development, etc.

(2) A language is composed of a sound system, a conceptual system, and a vocabulary and grammar system. All of these systems are highly complex and to a very large extent language-specific. Where do the very large number of building blocks making up these three systems come from? This question is traditionally addressed by historical linguists who have collected a huge set of examples and reconstructions of historical language change, identified universal trends of change (usually under the label of grammaticalization) [11], and proposed phylogenetic trees showing the cultural dependencies between languages and language families [10]. This effort has recently been complemented by research into causal and mechanistic models for these attested historical trends [19]. The models are formulated in terms of known characteristics of human information processing, the nature of human interaction patterns, the structure and change in human populations, and the changing communicative challenges that human societies may generate.

In this article, I am concerned with (2), i.e. the evolution of languages, because that is what the controversy is about: Does it make sense to speak about evolution in this case? In other words, is a language system exhibiting genuine (non-biological) evolution - which, I guess, we should then call cultural evolution even though there is apparently quite some resistance against using this term - or are languages merely 'recycling the limited alternatives that the biological envelope makes available' [4], p. 511, in other words, is language change only exhibiting random surface variations within the biologically heavily constrained framework of Universal Grammar?

In my own experience, the arguments against the evolutionary linguistics point of view are often based on a wrong (or one might say a different) conception of what the term evolution means. It is perhaps interesting to recall that Darwin did not use the term evolution at all in his book 'On the origins of species', but talked about transmutation instead, because evolution at that time meant either the unfolding of a predetermined plan, which Darwin wanted to put into question, or the gradual development of a system towards something better. The latter sense was used by philosophers such as Auguste Comte and Herbert Spencer in the context of the social sciences, emerging around the same time as Darwin wrote his key work (i.e. around 1850). However, the idea that evolution implies change towards a 'better' system is not at all implied by the contemporary notion of (biological) evolution - and it is not intended by evolutionary linguists when they use the term evolution.

Another misunderstanding, again coming from the usage of the word evolution in the social sciences, is that evolution implies some driving force. But, in the currently standard biological interpretation, the contrary is true. Biological change is emphatically not considered to be driven by a particular goal or an 'intelligent watchmaker' who designs and engineers change. The variation is basically 'blind' towards the goal of creating a more adaptive organism and the horse work is done by selection that picks out those variants that contribute to better adaptation.

A third reason why many linguists, even historical linguists, are weary of using the term evolution is because they underestimate the kind of novelty that may emerge in a language. Everybody agrees that there is an erosion of forms (as in the transformation of the Latin "vita" to "vida", then "vitha", "via", and finally "vie" in French) or surface shifts in specific morphological or syntactic patterns (as in the shift in Germanic languages from a tendency for an SOV (subject-object-verb) pattern to an SVO pattern). But there is also by necessity a process of renewal in meaning expression counterbalancing their loss. Renewal often starts from the recruitment of existing lexical materials, which turn into abstract syntactic patterns through semantic bleaching and routinization, then coalesce into morphological paradigms, before eroding again so that the cycle must restart. The expression of future is a well known meaning domain where historical linguists have observed these phenomena very clearly [6], although many other domains are equally illustrative. For the domain of future, we see that the Proto-Indo-European analytic expression "*kanta b^huti", literally 'sing be.3PS.SING' meaning 'he will sing', coalesced into the Latin "cantabi-t" (sing-3PS.SING) in which future is expressed morphologically using an affix attached to the stem. This mode of expression became replaced in late Latin with another analytic form: "cantare hab-et" (sing-INF have-3PS.SG), which coalesced again in French to become "chantera" (or Spanish "cantará") (sing.3PS.SING). And this synthetic expression was then replaced again with "(il) va chanter" (literally: 'he goes to sing' - but still meaning 'he will sing'). This kind of language innovations did not just happen in the past but are ongoing. They may include the emergence of entirely new syntactic categories (such as articles), new syntactic patterns (for example hierarchical phrase structure,[21]), new grammatical functions (such as information structure) and case roles, new semantic domains (like evidentials), new morphological paradigms (for example to express classifiers), as well as new sounds, sound complexes, new conceptual building blocks, and conceptualizations. The speed of these types of change is variable. Sometimes it goes very fast, possibly under the influence of rapid population change or intense language contact due to an invasion. At other times it goes much more slowly and may take centuries to complete.

How such innovations arise and spread in a population is the key question evolutionary linguists try to answer. And their key insight is that the same abstract principles contemporary biologists have been using with extraordinary success, namely replicator dynamics and level formation, are the most appropriate route to do so. What exactly is meant by replicator dynamics and level formation?

2. Replicator dynamics

The replicator dynamics model is based on Darwin's original insight into organismic evolution (i.e. species evolution). It has four ingredients:

1. A set of *units* carrying particular *traits*, for example, birds with a particular skin coloration. The units are sometimes called *interactors* [12], because they interact with the environment or with other units, or also *vehicles* [9], because they carry the traits.
2. The traits replicate and are therefore called *replicators*. There are multiple ways this can happen, but in organismic evolution, most traits replicate by the multiplication with inheritance of the units so that a whole set of traits gets copied from parent to offspring.
3. There must be a source of *variation* in the traits, for example due to mutation or recombination of the genes that influence the formation of the traits in offspring.
4. There must be a source of *selection*, having as a side effect that the frequency of those traits that contribute to a better selective fit increase in the population of units. In the original Darwinian model, selection is called 'natural' because it rests on the survival and fecundity of the units. For example, male birds with a particular coloration might be preferred by females or be less visible to predators and therefore have more offspring.

When these four elements are put into action in a particular environment, they lead to units that have traits adapted to that environment. So the replicator dynamics model couples the level of the individual with the level of the population.

This replicator dynamics model is universally accepted in biology and very well understood, both from a mathematical point of view [18] and - in the case of organismic evolution - also from a mechanistic point of view: Thanks to advances in molecular biology we know how Nature is able to construct new units from a genetic template explaining how multiplication with inheritance can be realized.

We know how the genetic material gets copied, how the mutations and recombinations that cause variation happen, how selection operates and affects changes in the frequency of traits.

It is important to realize that the replicator dynamics model is very general. For example, it accomodates horizontal transmission, Lamarckian sources of variation, epigenetics, random drift, niche construction, etc. [14]. Crucially, it can be instantiated in many different media. For example, replicator dynamics is now routinely instantiated in computers to 'evolve' complex programs known as genetic algorithms, in autonomous robots to evolve new bodies and control software, or in chemistry to evolve new compounds. The model is therefore a very powerful theory on how complexity may arise in systems without design or central coordination.

The question of interest here is of course how this model can help us to understand the evolution of languages. This requires that we need to find how the four key ingredients of the replicator dynamics model, namely units (interactors), traits (replicators), and variation and selection, can be instantiated for language. Here is a way to do this (see the table in Figure 1).

Replicator Model	**Species**	**Language**
Units (interactors)	organisms	language users
Traits (replicators)	features of organisms	language components
Replication	through genetic transmission	through social learning
Sources of variation	genetic mutation, recombination	learning, performance variation, innovation
Selection	survival and fecundity	communicative success, expressive power, cognitive effort

Figure 1: Organismic evolution and language are conceived as two instantiations of the same replicator dynamics model.

1. The units are speakers and listeners and the traits are the properties of their language systems that shape features of concrete utterances: speech sounds, conceptual structures, and relations between meaning and form. The latter includes vocabulary, such as for naming color categories, morphological paradigm, for example for expressing tense and aspect, syntactic structures, as for organizing the

main constituents in clauses, agreement systems, for example to constrain the referents of pronouns. A reasonable vocabulary, an inventory of idiomatic constructions, and a reasonable set of more abstract grammatical constructions requires most probably on the order of a few hundreds of thousands of quite complex form-meaning pairs. So we are talking about a system of significant size. In contrast to Croft [7] and most memetic approaches to language, I do not consider the replicating traits to be features of concrete utterances (Croft's linguemes), rather the replicators are the datastructures and cognitive processing mechanisms stored in individual brains that enable the production, recognition, and appropriate usage of these features in actual language use.

2. In the case of language, replication happens in two ways: either by social learning, when the speaker uses a component that is unknown to the listener and the listener forms an hypothesis and stores it, or by rehearsal, when the speaker or listener reuses an existing component in their linguistic interaction, so that this component is less likely to be forgotten.

3. The existence of variation in language use is well documented by sociolinguists, and there are multiple sources for it:

- It can easily arise during social learning because the learner overgeneralizes or overspecializes, infers meanings not intended by the speaker, or imposes an existing system, particularly in second language learning.
- Variation also arises through 'performance deviations', which are almost unavoidable given the incredible challenge of producing and comprehending spoken language. For example, the dental consonant /t/ is pronounced as /d/ between /i/ and /a/ because of rapid articulatory movement, case affixes are left out at the end of articles, a non-conventional constituent ordering is used in the main clause to topicalize another constituent than the subject.
- Variation arises furthermore through creative language use, i.e. innovations that speakers introduce to handle situations that are not yet covered by their existing system. This goes from the usage of an existing word for a new meaning, coercion of a word to have another grammatical function (e.g. a noun acts as a verb), the stretching of a grammatical construction to make it fit for a new purpose, etc.

A variant may be one-off or it may be stored, spread through social learning to other individuals and progressively become part of the shared language.

4. Is there selection in the case of language? Undeniably there is a lot of random change - but that happens in biological evolution as well, indeed that is

expected because some of the variation has no particular impact. On the other hand, it is not difficult to identify three important selectionist factors: reaching persistent communicative success, maintaining relevant expressive power, and reducing cognitive effort:

- *Communicative success* is the most important because it gives speaker and listener feedback on whether the component they used is part of the common language. It therefore directly impinges on replication: the more a particular grammatical construction was used successfully the more it will be reused, spread further in the population, and come to dominate competitors.

- *Increased expressive power* puts pressure on more innovation, whereas decay in the relevance of certain meanings causes the linguistic forms needed to express these meanings to fall out of usage and be forgotten.

- *Reducing cognitive effort* is needed to allow growth in complexity while coping with the amazing speed of language production and comprehension. It includes: preference for components that reduce combinatorial explosions in syntactic parsing and semantic interpretation, optimize memory access, routinize speech articulation and utterance planning, or minimize inventory and thus storage, for example by the reuse of existing elements for novel functions.

Obviously these three factors interact with each other. Reducing effort for the speaker may increase effort for the listener, up to a point where the utterance is too vague and semantically ambiguous and leads to communicative failure.

When these four model ingredients are in place, the replicator dynamics model predicts that a language system emerges with sufficient expressive power and adapted to the cognitive capacities of the brain, that it gets culturally transmitted across generations, and that the system keeps adapting to changing communicative needs. All this can be demonstrated conclusively using computer simulations and mathematical models based on evolutionary game theory [15].

Note that I do not use evolution here as a metaphor. Organismic evolution and language evolution are both instantiations of the same universal replicatory dynamics model, and other instantiations exist as well. Another point is that the model combines the individual and population views on language change. The representations, processing and learning strategies of individuals are modeled as one would in most approach to language, but their employment in a population of interacting individuals gives rise to language at the population level [16], [8].

3. Level Formation

Although replicator dynamics is best known, it is in itself not enough to explain the remarkable complexity of life and the transitions between simpler to more complex living forms. So evolutionary biology rests on a second pillar, which has gained attention only in the past few decades, namely *level formation*, also known as transition theory [20] or social evolution theory [3]. Level formation attempts to explain the formation of hierarchical levels, for example, how there can be an evolution from autonomous single cells to multi-cellular structures, or from autonomous insects to insect colonies. It postulates a stage where individual units aggregate causing new traits to emerge, amplified through self-organisation. Then there is typically a specialization of function, including typically a loss of individuality or the ability to multiply autonomously. The hierarchical unit then starts to undergo replicator dynamics in its own right: units multiply with inheritance and variation, they undergo selection, and those emergent traits that provide more adaptation proliferate. When there are units at several levels thus formed, multi-level selection becomes important.

Level formation is clearly also relevant in the case of language. We see the formation of higher level units: individual sounds aggregate into syllable clusters and larger supra-segmental units. Lexical stems and affixes cluster in words, words in phrases, and phrases in higher order phrases. Sentences group into textual units and dialog patterns. Primitive semantic building blocks, such as semantic categories, become part of more complex conceptualizations which involve set operations, perspective taking, higher order categories, frame-like structures, etc. Although level formation is also needed to understand the full extent how languages evolve, it goes beyond the scope of this short discussion paper to work this hypothesis out in more detail here.

4. Conclusions

Once the core of contemporary evolutionary theory, namely replicator dynamics and level formation, is understood and properly instantiated for language, many puzzles why and how languages change fall into place. We understand why there is so much variation across different languages and within a language community, even within the language use of a single speaker. We understand how a language community can reach coherence even if there is no central authority, or how innovations can arise, spread and become dominant. The evolutionary linguistics view described here is entirely compatible with the data and generalizations that have been amassed by historical linguists.

Importantly, the evolutionary perspective leads to a revision of many other aspects of linguistic theory. Instead of only focusing on cataloging the possible elements that may occur in a language, we are invited to inquire where these elements come from. And rather than assuming that a language user only has to know a single static language system, we are invited to inquire what cognitive mechanisms allow speakers and listeners to participate in the linguistic evolutionary dynamics, how social learning takes place, how language users can maintain and keep track of variation in language use, how communicative success feeds back into memory changes so that 'more adapted' linguistic expressions proliferate, and, most fascinating of all, how new linguistic innovations may arise and spread.

5. Acknowledgement

The author is a research professor at the Institute for Advanced Studies in Barcelona (ICREA) associated with the Institut de Biologia Evolutiva (UPF-CSIC). The support of both institutions is strongly acknowledged. Work on this paper was made possible by additional funding from the European FP7 project Insight and from the Wissenschaftskolleg in Berlin.

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Experimental and Theoretical Approaches to Conscious Processing

Stanislas Dehaene[1,2,3,4,*] and Jean-Pierre Changeux[4,5,*]
[1]INSERM, Cognitive Neuroimaging Unit, Gif sur Yvette, 91191 France
[2]CEA, DSV, I2BM, Neurospin center, Gif sur Yvette, 91191 France
[3]University Paris 11, Orsay 91401, France
[4]Collège de France, 11 Place Marcelin Berthelot, 75005 Paris, France
[5]Institut Pasteur CNRS URA 2182, Institut Pasteur, 75015 Paris, France
*Correspondence: stanislas.dehaene@gmail.com (S.D.), changeux@noos.fr (J.-P.C.)
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Recent experimental studies and theoretical models have begun to address the challenge of establishing a causal link between subjective conscious experience and measurable neuronal activity. The present review focuses on the well-delimited issue of how an external or internal piece of information goes beyond nonconscious processing and gains access to conscious processing, a transition characterized by the existence of a reportable subjective experience. Converging neuroimaging and neurophysiological data, acquired during minimal experimental contrasts between conscious and nonconscious processing, point to objective neural measures of conscious access: late amplification of relevant sensory activity, long-distance cortico-cortical synchronization at beta and gamma frequencies, and "ignition" of a large-scale prefronto-parietal network. We compare these findings to current theoretical models of conscious processing, including the Global Neuronal Workspace (GNW) model according to which conscious access occurs when incoming information is made globally available to multiple brain systems through a network of neurons with long-range axons densely distributed in prefrontal, parieto-temporal, and cingulate cortices. The clinical implications of these results for general anesthesia, coma, vegetative state, and schizophrenia are discussed.

Introduction

Understanding the neuronal architectures that give rise to conscious experience is one of the central unsolved problems of today's neuroscience, despite its major clinical implications for general anesthesia, coma, vegetative-state, or minimally conscious patients. The difficulties are numerous. Notably, the term "consciousness" has multiple meanings, most of which are difficult to precisely define in a manner amenable to experimentation. In this review, we outline recent advances made in understanding the delimited issue of conscious access: how does an external or internal piece of information gain access to conscious processing, defined as a reportable subjective experience?

We start with a brief overview of the relevant vocabulary and theoretical concepts. We then examine the experimental studies that have attempted to delineate the objective physiological mechanisms of conscious sensory perception by contrasting it with minimally different, yet nonconscious processing conditions, using a variety of methods: behavior, neuroimaging, time-resolved electro- and magneto-encephalography, and finally single-cell electrophysiology and pharmacology. We critically examine how the present evidence fits or argues against existing models of conscious processing, including the Global Neuronal Workspace (GNW) model. We end by examining possible consequences of these advances for pathological brain states, including general anesthesia, coma, and vegetative states.

I. Vocabulary and Major Experimental Paradigms

Conscious State versus Conscious Contents

"Conscious" is an ambiguous word. In its intransitive use (e.g., "the patient was still conscious"), it refers to the *state of consciousness*, also called *wakefulness* or *vigilance*, which is thought to vary almost continuously from coma and slow-wave sleep to full vigilance. In its transitive use (e.g., "I was not conscious *of* the red light"), it refers to *conscious access* to and/or *conscious processing* of a specific piece of information. The latter meaning is the primary focus of this review. At any given moment, only a limited amount of information is consciously accessed and defines the current *conscious content*, which is reportable verbally or by an intended gesture. At the same time, many other processing streams co-occur but remain *nonconscious*.

Major Experimental Paradigms

A broad variety of paradigms (reviewed in Kim and Blake, 2005) are now available to create a minimal contrast between conscious and nonconscious stimuli (Baars, 1989) and thus isolate the moment and the physiological properties of conscious access. A basic distinction is whether the nonconscious stimulus is *subliminal* or *preconscious* (Dehaene et al., 2006; Kanai et al., 2010). A *subliminal* stimulus is one in which the bottom-up, stimulus-driven information is so reduced as to make it undetectable, even with focused attention. A *preconscious* stimulus, by contrast, is one that is potentially *visible* (its energy and duration are such that it could be seen), but which, on a given trial, is not consciously perceived due to temporary distraction or inattention.

Subliminal presentation is often achieved by *masking*, a method whereby the subjective visibility of a stimulus is reduced or eliminated by the presentation, in close spatial and temporal contiguity, of other stimuli acting as "masks" (Breitmeyer, 2006). For instance, a word flashed for 33 ms is visible when presented in isolation but becomes fully invisible when preceded and followed by geometrical shapes. Masked stimuli are frequently used to induce *subliminal priming*, the facilitation of the processing of a visible target by the prior presentation of an identical or related subliminal prime (for review, see Kouider and Dehaene, 2007). Subliminal presentation can also be achieved with *threshold* stimuli, where the contrast or energy of a stimulus is progressively reduced until its presence is unnoticeable. *Binocular rivalry* is another common paradigm whereby the image in one eye becomes subliminal by competition with a rivaling image presented in the other eye. Participants typically report temporal alternations in the image that is consciously perceived. However, a variant of binocular rivalry, the *continuous flash suppression* paradigm allows an image to be made permanently invisible by presenting continuously flashing shapes in the other eye (Tsuchiya and Koch, 2005).

An equally large range of techniques allows for *preconscious* presentation. In *inattentional blindness*, a potentially visible but unexpected stimulus remains unreported when the participants' attention is focused on another task (Mack and Rock, 1998; Simons and Ambinder, 2005). The *attentional blink* (AB) is a short-term variant of this effect where a brief distraction by a first stimulus T1 prevents the conscious perception of a second stimulus T2 briefly presented within a few hundreds of milliseconds of T1 (Raymond et al., 1992). In the related *psychological refractory period* (PRP) effect (Pashler, 1994; Welford, 1952), T2 is unmasked and is therefore eventually perceived and processed, but only after a delay during which it remains nonconscious (Corallo et al., 2008; Marti et al., 2010). The "distracting" event T1 can be a surprise event that merely captures attention (Asplund et al., 2010). The minimum requirement, in order to induce AB, appears to be that T1 is consciously perceived (Nieuwenstein et al., 2009). Thus, PRP and AB are closely related phenomena that point to a serial limit or "bottleneck" in conscous access (Jolicoeur, 1999; Marti et al., 2010; Wong, 2002) and can be used to contrast the neural fate of two identical stimuli, only one of which is consciously perceived (Sergent et al., 2005).

Objective versus Subjective Criteria for Conscious Access

How can an experimenter decide whether his experimental subject was or was not conscious of a stimulus? According to a long psychophysical tradition, grounded in signal-detection theory, a stimulus should be accepted as nonconscious only if subjects are unable to perform above chance on some direct task of stimulus detection or classification. This strict *objective criterion* raises problems, however (Persaud et al., 2007; Schurger and Sher, 2008). First, it tends to overestimate conscious perception: there are many conditions in which subjects perform better than chance, yet still deny perceiving the stimulus. Second, performance can be at chance level for some tasks, but not others, raising the issue of which tasks count as evidence of conscious perception or merely of subliminal processing. Third, the approach requires accepting the null hypothesis of chance-level performance, yet performance never really falls down to zero, and whether it is significant or not often depends on arbitrary choices such as the number of trials dedicated to its measurement.

For these reasons, recent alternative approaches emphasize either pure subjective reports, such as ratings of stimulus visibility (Sergent and Dehaene, 2004), or second-order commentaries such as postdecision wagering (e.g., would you bet that your response was correct?; Persaud et al., 2007). The wagering method and related confidence judgements provide a high motivation to respond truthfully and in an unbiased manner (Schurger and Sher, 2008). Furthemore, they can be adapted to nonhuman subjects (Kiani and Shadlen, 2009; Terrace and Son, 2009). However, they can sometimes exceed chance level even when subjects deny seeing the stimulus (Kanai et al., 2010). Conversely, subjective report is arguably the primary data of interest in consciousness research. Furthermore, reports of stimulus visibility can be finely quantified, leading to the discovery that conscious perception can be "all-or-none" in some paradigms (Del Cul et al., 2007; Del Cul et al., 2006; Sergent and Dehaene, 2004). Subjective reports also present the advantage of assessing conscious access immediately and on every trial, thus permitting postexperiment sorting of conscious versus nonconscious trials with identical stimuli (e.g., Del Cul et al., 2007; Lamy et al., 2009; Pins and Ffytche, 2003; Sergent et al., 2005; Wyart and Tallon-Baudry, 2008).

Although the debate about optimal measures of conscious perception continues, it is important to acknowledge that objective assessments, wagering indices and subjective reports are generally in excellent agreement (Del Cul et al., 2006; Del Cul et al., 2009; Persaud et al., 2007). For instance, in visual masking, the conscious perception thresholds derived from objective and subjective data are essentially identical across subjects (r^2 = 0.96, slope $\approx$ 1) (Del Cul et al., 2006). Those data suggest that conscious access causes a major change in the global availability of information, whether queried by objective or by subjective means, whose mechanism is the focus of the present review.

Selective Attention versus Conscious Access

Conscious access must be distinguished from the related concept of *attention*. William James (1890) provided a well-known definition of attention as "the taking possession by the mind, in clear and vivid form, of one out of what seem several simultaneously possible objects or trains of thought." The problem with this definition is that it conflates two processes that are now clearly separated in cognitive psychology and cognitive neuroscience (e.g., Huang, 2010; Posner and Dehaene, 1994): *selection* and *access*. *Selection*, also called *selective attention*, refers to the separation of relevant versus irrelevant information, isolation of an object or spatial location, based on its saliency or relevance to current goals, and amplification of its sensory attributes. *Access* refers to its conscious "taking possession of the mind"—the subject of the present review.

Empirical evidence indicates that selection can occur without conscious processing (Koch and Tsuchiya, 2007). For instance, selective spatial attention can be attracted to the location of a target stimulus that remains invisible (Bressan and Pizzighello, 2008; McCormick, 1997; Robitaille and Jolicoeur, 2006; Woodman and Luck, 2003). Selective attention can also amplify the processing of stimuli that remain nonconscious (Kentridge et al., 2008; Kiefer and Brendel, 2006; Naccache et al., 2002). Finally, in simple displays with a single target, conscious access can occur independently of selection (Wyart and Tallon-Baudry, 2008). In cluttered displays, however, selection appears to be a prerequisite of conscious access: when faced with several competing stimuli, we need attentional selection in order to gain conscious access to just one of them (Dehaene and Naccache, 2001; Mack and Rock, 1998). These findings indicate that *selective attention* and *conscious access* are related but dissociable concepts that should be carefully separated, attention frequently serving as a "gateway" that regulates which information reaches conscious processing.

II. Experimental Studies of the Brain Mechanisms of Conscious Access

With this vocabulary at hand, we turn to empirical studies of conscious access. The simplest experiments consist in presenting a brief sensory stimulus that is sometimes consciously accessible, sometimes not, and using behavior, neuroimaging, and neurophysiological recording to monitor the depth of its processing and how it differs as a function of conscious reportability.

Experiments Contrasting Visible and Invisible Stimuli

Behavioral evidence. A visual stimulus that is masked and remains invisible can nevertheless affect behavior and brain activity at multiple levels (for review, see Kouider and Dehaene, 2007; Van den Bussche et al., 2009b). Subliminal priming has now been convincingly demonstrated at visual, semantic, and even motor levels. For instance, when a visible target image is preceded by a subliminal presentation of the same image, simple decisions, such as judging whether it refers to an object or animal, are accelerated compared to when the image is not repeated. Crucially, this repetition effect resists major changes in the physical stimulus, such as presenting the same word in upper case versus lower case (Dehaene et al., 2001) or presenting the same face in two different orientations (Kouider et al., 2009), suggesting that invariant visual recognition can be achieved without awareness. At the semantic level, subliminal extraction of the meaning of words has now been demonstrated for a variety of word categories (e.g., Gaillard et al., 2006; Naccache and Dehaene, 2001; Van den Bussche et al., 2009a). At even more advanced levels, a subliminal stimulus can bias motor responses (Dehaene et al., 1998b; Leuthold and Kopp, 1998). Subliminal monetary incentives enhance subjects' motivation in a demanding force task, indicating that motivation is modulated by nonconscious signals (Pessiglione et al., 2007). So is task setting: masked shapes can act as cues for task switching and lead to detectable changes in task set (Lau and Passingham, 2007). Even inhibitory control can be partially launched nonconsciously, as when a nonconscious "stop" signal slows down or interrupts motor responses (van Gaal et al., 2008) (see Figure 1).

The above list suggests that entire chains of specialized processors can be subject to nonconscious influences. Nevertheless, three potential limits to subliminal processing have been identified (Dehaene and Naccache, 2001). First, subliminal priming quickly *decreases with processing depth*, such that only small influences are detectable at higher cognitive and decision levels (Dehaene, 2008; van Gaal et al., 2008). For instance, a subliminal number can enter into a single numerical operation, but not a series of two arbitrary operations (Sackur and Dehaene, 2009). Second, subliminal priming *decreases with elapsed time*, and therefore typically ceases to be detectable after 500 ms (Dupoux et al., 2008; Greenwald et al., 1996; Mattler, 2005). For instance, classical conditioning across a temporal gap only obtains when participants report being aware of the relations among the stimuli (Clark et al., 2002) (although see Bekinschtein et al., 2009b). Third, subliminal stimuli typically fail to yield lasting and flexible modifications in *executive control*. Human subjects generally excel in identifying strategies that exploit virtually any statistical relation among stimuli, but such strategic control appears to require consciousness (Posner et al., 1975/2004) and is not deployed when the stimuli are masked or unattended and therefore are not consciously detected (Heinemann et al., 2009; Kinoshita et al., 2008; Merikle and Joordens, 1997; Van den Bussche et al., 2008). For instance, under conscious conditions, subjects typically slow down after a conflict or error trial but may not do so when the error or conflict is nonconscious (Kunde, 2003; Nieuwenhuis et al., 2001) (for two interesting exceptions, see Logan and Crump, 2010; van Gaal et al., 2010).

Brain-scale neuroimaging. Functional magnetic resonance imaging (fMRI) can provide a global image of the brain activity evoked by a visible or invisible stimulus, integrated over a few seconds. Grill-Spector et al. (2000) first used fMRI to measure visual activity evoked by masked pictures presented below or above the visibility threshold. Activation of the primary visual area V1 was largely unaffected by masking, but the amount of activation in more anterior regions of lateral occipital and fusiform cortex strong correlated with perceptual reports. A year later (Dehaene et al., 2001), a similar contrast between masked and unmasked words, now at the whole-brain level, again revealed a strong correlation of conscious perception with fusiform activity, but also demonstrated extended areas of activation uniquely evoked by conscious words, including inferior prefrontal, mesial frontal, and parietal sites (Figure 1). In more recent fMRI work, using a masking paradigm where conscious reports followed a characteristic U-shaped curve as a function of the target-mask delay, fusiform and midline prefrontal and inferior parietal regions again closely tracked conscious perception (Haynes et al., 2005b). An important control was recently added: participants' objective performance could be equated while subjective visibility was manipulated (Lau and Passingham, 2006). In this case, a correlate of visibility could only be detected in left dorsolateral prefrontal cortex.

Some authors have found correlations of fMRI activation with visibility of masked versus unmasked stimuli exclusively in posterior visual areas (e.g., Tse et al., 2005). However, in their paradigm, even the unmasked stimuli were probably not seen because they were unattended and irrelevant, which can prevent conscious access (Dehaene et al., 2006; Kouider et al., 2007; Mack and Rock, 1998). Overall, fMRI evidence suggests two convergent correlates of conscious access: (1) amplification of activity in visual cortex, clearest in higher-visual areas such as the fusiform gyrus, but possibly including earlier visual areas

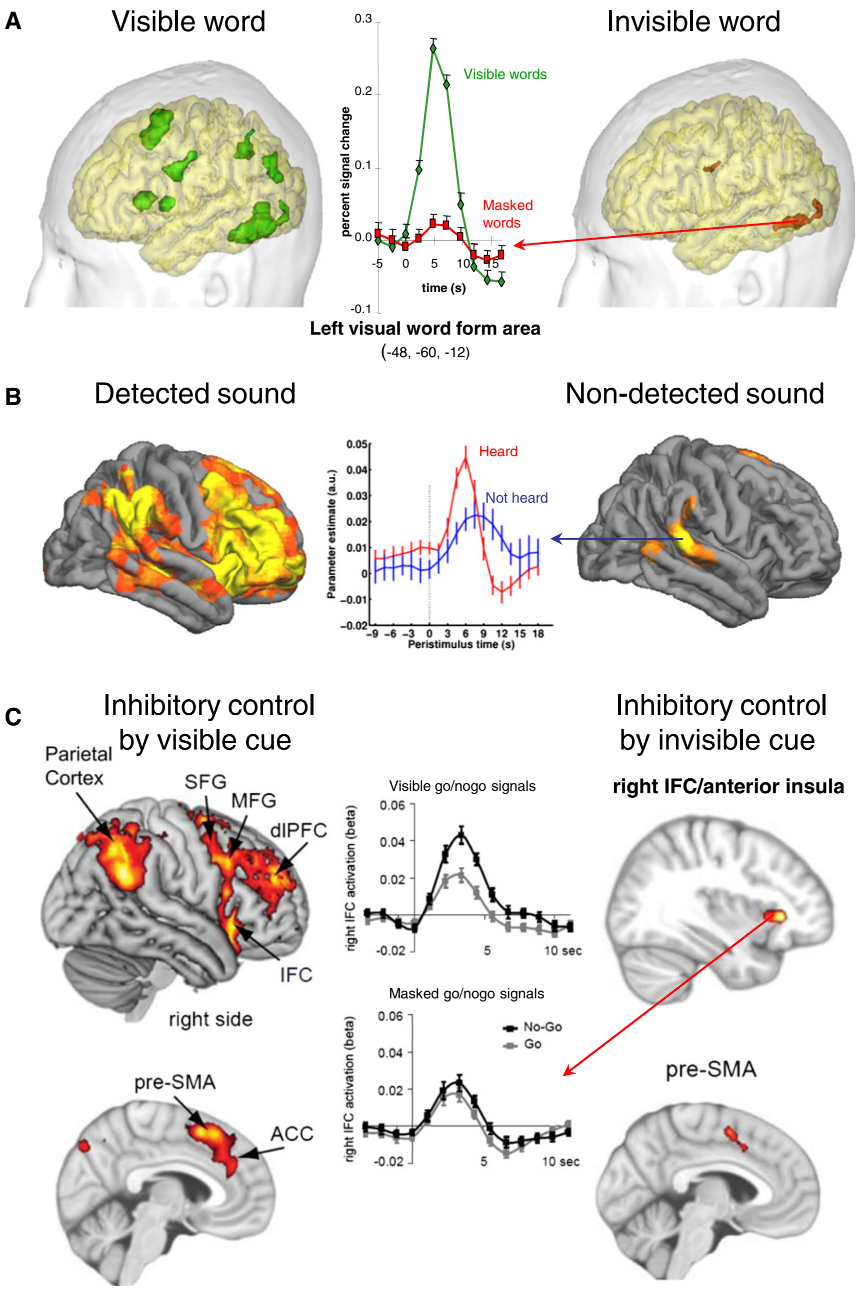

Figure 1. fMRI Measures of Conscious Access

(A) An early fMRI experiment contrasting the fMRI activations evoked by brief presentations of words that were either readable (left) or made invisible by masking (right) (adapted from Dehaene et al., 2001). Nonconscious word processing activated the left occipito-temporal visual word form area, but conscious perception was characterized by (a) an intense amplification of activation in relevant nonconscious processors, here the visual word form area (left occipito-temporal cortex; see middle graph); (b) an additional spread of activation to a distributed, though restricted set of associative cortices including inferior parietal, prefrontal, and cingulate areas.

(B) fMRI study of threshold-level noises, approximately half of which were consciously detected (Sadaghiani et al., 2009). Bilateral auditory areas showed a nonconscious activation, which was amplified and spread to distributed inferior parietal, prefrontal, and cingulate areas (for similar results with tactile stimuli, see Boly et al., 2007).

(C) fMRI study of inhibitory control by a visible or invisible cue (van Gaal et al., 2011). Subjects were presented with masked visual shapes, at the threshold for conscious perception, some of which occasionally required inhibiting a response (go/no-go task). Small activations to the nonconscious no-go signal were detected in the inferior frontal and preSMA cortices, but inhibitory control by a conscious no-go signal was associated with fMRI signal amplification (see the difference between no-go and go signals in middle graphs), and massive spread of the activation to additional and more anterior areas including prefrontal, anterior cingulate, and inferior parietal cortices.

(e.g., Haynes et al., 2005a; Polonsky et al., 2000; Williams et al., 2008); (2) emergence of a correlated distributed set of areas, virtually always including bilateral parietal and prefrontal cortices (see Figure 1).

Time-resolved imaging methods. Event-related potentials (ERPs) and magneto-encephalography (MEG) are noninvasive methods for monitoring at a millisecond scale, respectively, the electrical and magnetic fields evoked by cortical and subcortical sources in the human brain. Both techniques have been used to track the processing of a masked stimulus in time as it crosses or does not cross the threshold for subjective report. In the 1960s already, ERP studies showed that early visual activation can be fully preserved during masking (Schiller and Chorover, 1966). This early finding has been supported by animal electrophysiology (Bridgeman, 1975, 1988; Kovács et al., 1995; Lamme et al., 2002; Rolls et al., 1999) and by essentially all recent ERP and MEG studies (Dehaene et al., 2001; Del Cul et al., 2007; Fahrenfort et al., 2007; Koivisto et al., 2006, 2009; Lamy et al., 2009; Melloni et al., 2007; Railo and Koivisto, 2009; van Aalderen-Smeets et al., 2006). Evidence from the attentional blink also confirms that the first 200 ms of initial visual processing can be fully preserved on trials in which subjects deny seeing a stimulus (Sergent et al., 2005; Vogel et al., 1998) (see Figure 2).

In ERPs, the most consistent correlate of visibility appears to be a late (~300–500 ms) and broadly distributed positive component called P3 or sometimes P3b (to distinguish it from the focal anterior P3a, which is thought to reflect automatic attention attraction and can occur nonconsciously [e.g., Muller-Gass et al., 2007; Salisbury et al., 1992]). A similarly slow and late waveform is seen in MEG (van Aalderen-Smeets et al., 2006). The generators of the P3b ERP have been shown by intracranial

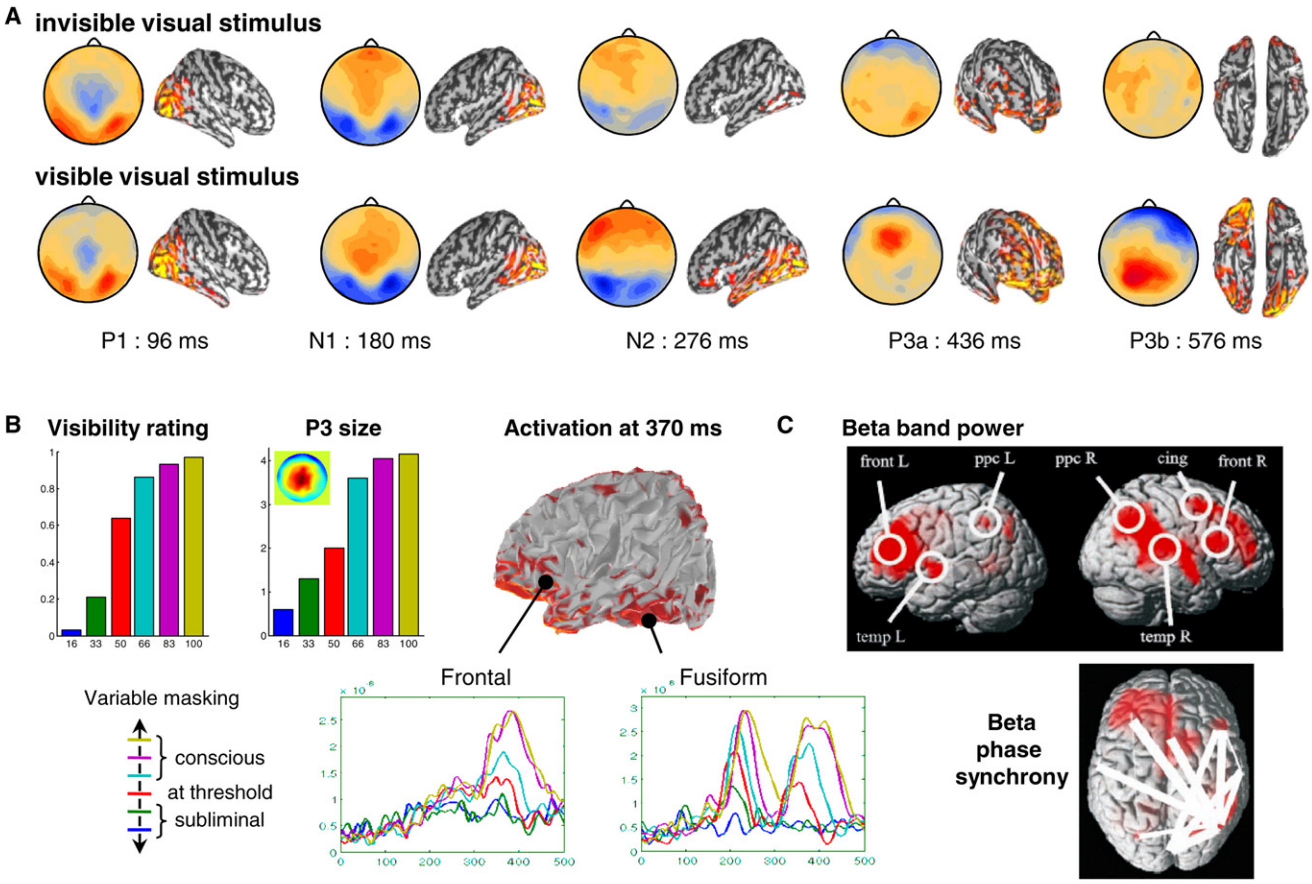

Figure 2. Electro- and Magneto-encephalography Measures of Conscious Access

(A) Time course of scalp event-related potentials evoked by an identical visual stimulus, presented during the attentional blink, as a function of whether it was reported as seen or unseen (Sergent et al., 2005). Early events (P1 and N1) were strictly identical, but the N2 event was amplified and the P3 events (P3a and P3b) were present essentially only during conscious perception.

(B) Manipulation of visibility by varying the temporal asynchrony between a visual stimulus and a subsequent mask (Del Cul et al., 2007). A nonlinearity, defining a threshold value for conscious access, was seen in both subjective visibility reports and the P3b event amplitude. Source modeling related this P3b to a sudden nonlinear ignition, about 300 ms after stimulus presentation, of distributed sources including inferior prefrontal cortex, with a simultaneous reactivation of early visual areas. Note the two-stage pattern of fusiform activation, with an early linear activation followed by a late nonlinear ignition.

(C) Magneto-encephalography correlates of the attentional blink (Gross et al., 2004). On perceived trials, induced power and phase synchrony increased in the low beta band (13–18 Hz), in a broad network dominated by right inferior parietal and left prefrontal sites.

recordings and ERP-fMRI correlation to involve a highly distributed set of nearly simultaneous active areas including hippocampus and temporal, parietal, and frontal association cortices (Halgren et al., 1998; Mantini et al., 2009). The P3b has been reproducibly observed as strongly correlated with subjective reports, both when varying stimulus parameters (e.g., Del Cul et al., 2007) and when comparing identical trials with or without conscious perception (e.g., Babiloni et al., 2006; Del Cul et al., 2007; Fernandez-Duque et al., 2003; Koivisto et al., 2008; Lamy et al., 2009; Niedeggen et al., 2001; Pins and Ffytche, 2003; Sergent et al., 2005) (however, this effect may disappear when the subject already has a conscious working memory representation of the target: Melloni et al., 2011). The effect is not easily imputable to increased postperceptual processing or other task confounds, as many studies equated attention and response requirements on conscious and nonconscious trials (e.g., Del Cul et al., 2007; Gaillard et al., 2009; Lamy et al., 2009; Sergent et al., 2005). For instance, Lamy et al. (2009) compared correct aware versus correct unaware trials in a forced-choice localization task on a masked stimulus, thus equating for stimuli and responses, and again observed a tight correlation with the P3b component.

Human ERP and MEG recordings also revealed that conscious perception is also accompanied, during a similar time window, by increases in the power of high-frequency fluctuations, primarily in the gamma band (>30 Hz), as well as their phase synchronization across distant cortical sites (Doesburg et al., 2009; Melloni et al., 2007; Rodriguez et al., 1999; Schurger et al., 2006; Wyart and Tallon-Baudry, 2009). In lower frequencies belonging to the alpha and low beta bands (10–20 Hz), the data are more ambiguous, as both power increases (Gross et al., 2004) and decreases (Gaillard et al., 2009; Wyart and Tallon-Baudry, 2009) have been reported, perhaps due to paradigm-dependent variability in the deployment of dorsal parietal attention networks associated with decreases in alpha-band power (Sadaghiani et al., 2010). Even when power decreases in these low frequencies, however, their

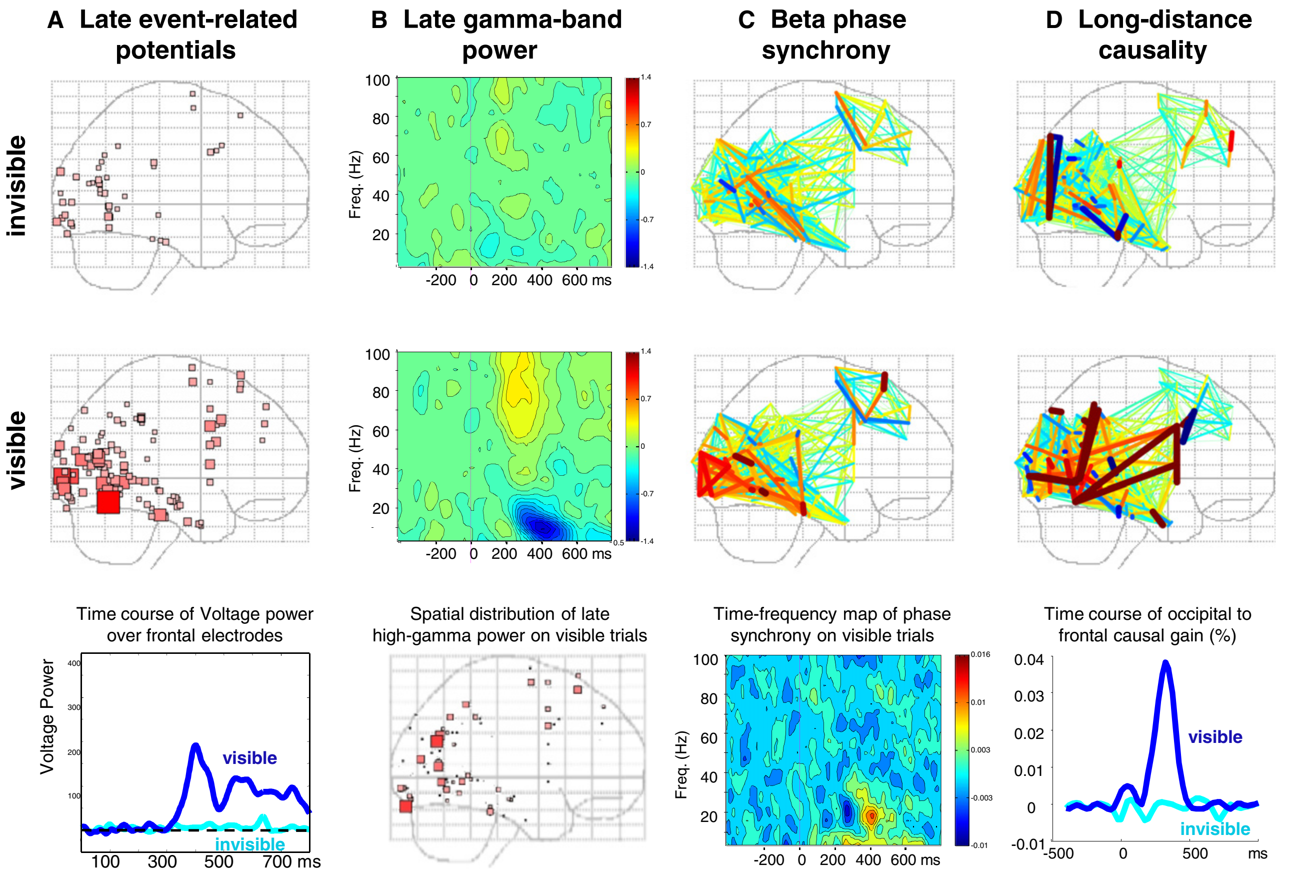

Figure 3. Intracranial Potentials during Conscious Access

Intracranial local-field potentials were recorded during stimulation with masked or unmasked words from a total of ten patients implanted with deep intracortical electrodes (Gaillard et al., 2009). Four intracranial signatures of conscious access were identified.

(A) Although invisible words elicited event-related potentials, mostly early (<300 ms) and at posterior sites, only visible words elicited massive and durable voltages in a late time window, particularly from the few available frontal electrodes.

(B) Gamma-band power increases were detectable for invisible words, but in a late time window (>300 ms) gamma power was massively amplified when the words were visible, particularly in the high-gamma range (50–100 Hz). Reduced power was seen in the alpha and lower beta bands.

(C) Phase synchrony increased for invisible words in a late time window (300–500 ms) in the beta frequency range (13–30 Hz).

(D) Causal relations across distant electrodes, assessed by Granger causality gain due to word presence, increased massively during the same time window. The bottom row shows causal gain for a particular electrode pair as a function of time. Increases were bidirectional but dominant in the bottom-up direction (e.g., occipital-to-frontal), compatible with the idea of posterior information "accessing" more anterior sites. All time scales are relative to stimulus onset.

long-distance phase synchrony is consistently increased during conscious perception (Gaillard et al., 2009; Gross et al., 2004; see also Hipp et al., 2011). The globally distributed character of these power and synchrony increases seems essential, because recent results indicate that *localized* increases in these parameters can be evoked by nonconscious stimuli, particularly during the first 200 ms of stimulus processing (Fisch et al., 2009; Gaillard et al., 2009; Melloni et al., 2007). Thus, short-lived focal increases in gamma-band power are not unique to conscious states but track activation of both conscious and nonconscious local cortical circuits (Ray and Maunsell, 2010). However, their significant enhancement on consciously perceived trials, turning into an all-or-none pattern after 200 ms, appears as a potentially more specific marker of conscious access (Fisch et al., 2009; Gaillard et al., 2009).

The high spatial precision and signal-to-noise ratio afforded by intracranial recording in epileptic patients provides essential data on this point. Gaillard et al. (2009) contrasted the fate of masked (subliminal) versus unmasked (conscious) words while recording from a total of 176 local sites using intracortical depth electrodes in ten epileptic patients. Four objective signatures of conscious perception were identified (Figure 3): (1) late (>300 ms) and distributed event-related potentials contacting sites in prefrontal cortex; (2) large and late (>300 ms) increases in induced power (indexing local synchrony) in high-gamma frequencies (50–100 Hz), accompanied by a decrease in lower-frequency power (centered around 10 Hz); (3) increases in long-distance cortico-cortical synchrony in the beta frequency band 13–30 Hz; (4) increases in causal relations among distant cortical areas, bidirectionally but more strongly in the bottom-up direction (as assessed by Granger causality, a statistical technique that measures whether the time course of signals at one site can forecast the future evolution of signals at another distant site). Gaillard et al. (2009) noted that all four signatures coincided

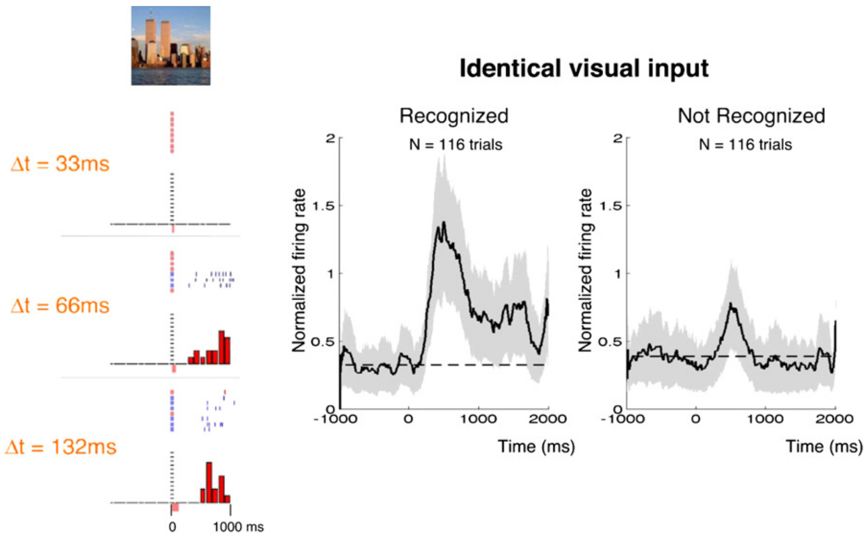

Figure 4. Human Single-Cell Recordings during Conscious Access

Single cells were recorded from the human medial temporal lobe and hippocampus during presentation of masked pictures, with a variable target-mask delay (Quiroga et al., 2008). The example at left shows a single cell that fired specifically to pictures of the World Trade Center, and did so only on trials when the patient recognized the picture (dark blue raster plots), not on trials when recognition failed (red raster plots). Graphs at right show the average firing rate across all neurons. Although a small transient firing could be seen on unrecognized trials, conscious perception was characterized by a massive and durable amplification of activity (for complementary results using electrocorticography (ECoG) in human occipito-temporal areas, see also Fisch et al., 2009).

in the same time window (300–500 ms) and suggested that they might constitute different measures of the same state of distributed "ignition" of a large cortical network including prefrontal cortex. Indeed, seen stimuli had a global impact on late evoked activity virtually anywhere in the cortex: 68.8% of electrode sites, although selected for clinical purposes, were modulated by the presence of conscious words (as opposed to 24.4% of sites for nonconscious words).

Neuronal recordings. A pioneering research program was conducted by Logothetis and collaborators using monkeys trained to report their perception during binocular rivalry (Leopold and Logothetis, 1996; Sheinberg and Logothetis, 1997; Wilke et al., 2006). By recording from V1, V2, V4, MT, MST, IT, and STS neurons and presenting two rivaling images, only one of which led to high neural firing, they identified a fraction of cells whose firing rate increased when their preferred stimuli was perceived, thus participating in a conscious neuronal assembly. The proportion of such cells increased from about 20% in V1/V2 to 40% in V4, MT, or MST to as high as 90% in IT and STS. This finding supports the hypothesis that subjective perception is associated with distributed cell assemblies whose neurons are denser in higher associative cortices than in primary and secondary visual cortices. Surprisingly, fMRI signals correlated quite strongly with conscious perception during rivalry in area V1 (Haynes and Rees, 2005; Polonsky et al., 2000) and even in the lateral geniculate nucleus of the thalamus (Haynes et al., 2005a; Wunderlich et al., 2005). The discrepancy between fMRI and single-cell recordings was addressed in a recent electrophysiological study (Maier et al., 2008; see also Wilke et al., 2006): within area V1 of the same monkeys, fMRI signals and low-frequency (5–30 Hz) local field potentials (LFPs) correlated with subjective visibility while high-frequency (30–90 Hz) LFPs and single-cell firing rate did not. One interpretation of this finding is that V1 neurons receive additional top-down synaptic signals during conscious perception compared to nonconscious perception, although these signals need not be translated into changes in average firing rate (Maier et al., 2008).

The masking paradigm afforded a more precise measurement of the timing of conscious information progression in the visual system. In area V1, multiunit recordings during both threshold judgments (Supèr et al., 2001) and masking paradigms (Lamme et al., 2002) identified two successive response periods. The first period was phasic, was time-locked to stimulus onset, and reflected objective properties such as stimulus orientation, whether or not they were detectable by the animal. The second period was associated with a late, slow, and long-lasting amplification of firing rate, called figure-ground modulation because it was specific to neurons whose receptive field fell on the foreground "figure" part of the stimulus. Crucially, only this second phase of late amplification correlated tightly with stimulus detectability in awake animals (Lamme et al., 2002; Supèr et al., 2001) and vanished under anesthesia (Lamme et al., 1998). Thus, although different forms of masking can affect both initial and late neural responses (Macknik and Haglund, 1999; Macknik and Livingstone, 1998), the work of Lamme and colleagues suggests that it is the late sustained phase that is most systematically correlated with conscious visibility. A similar conclusion was reached from earlier recordings in inferotemporal cortex (Kovács et al., 1995; Rolls et al., 1999) and frontal eye fields (Thompson and Schall, 1999, 2000).

Only a single study to date has explored single-neuron responses to seen or unseen stimuli in human cortex (Quiroga et al., 2008). Pictures followed at a variable delay by a mask were presented while recording from the antero-medial temporal lobe in five patients with epilepsy. A very late response was seen, peaking around 300 ms and extending further in time. This late firing reflected tightly the person's subjective report, to such an extent that individual trials reported as seen or unseen could be categorically distinguished by the neuron's firing train (see Figure 4). Such a late categorical response is consistent with the hypothesis that conscious access is "all-or-none," leading either to a high degree of reverberation in higher association cortex (conscious trial) or to a vanishing response (Dehaene et al., 2003b; Sergent et al., 2005; Sergent and Dehaene, 2004).

Single-cell electrophysiology has also contributed to a better description of the postulated role of synchrony in conscious perception (Rodriguez et al., 1999; Varela et al., 2001). Within a single area such as V4, the degree to which single neurons synchronize with the ongoing fluctuations in local-field potential is a predictor of stimulus detection (Womelsdorf et al., 2006). Across distant areas such as FEF and V4 (Gregoriou et al., 2009) or PFC and LIP (Buschman and Miller, 2007), synchrony is enhanced when the stimulus in the receptive field is attended and is thus presumably accessed consciously. Consistent with human MEG and intracranial studies (e.g., Gaillard et al., 2009; Gross et al., 2004), synchronization involves both gamma and beta bands, the latter being particularly enhanced during top-down attention (Buschman and Miller, 2007). During the late phase of attention-driven activity, causal relations between distant areas are durably enhanced in both directions, but more strongly so in the bottom-up direction from V4 to FEF (Gregoriou et al., 2009), again similar to human findings (Gaillard et al., 2009) and compatible with the idea that sensory information needs to be propagated anteriorily, particularly to PFC, before becoming consciously reportable.

Experiments with Perceived and Unperceived Stimuli outside the Visual Modality

Although vision remains the dominant paradigm, remarkably similar signatures of conscious access have been obtained in other sensory or motor modalities (see Figure 1).

In the *tactile* modality, threshold-level stimuli were studied both in humans with fMRI and magneto-encephalography (Boly et al., 2007; Jones et al., 2007) and in awake monkeys with single-cell electrophysiology (de Lafuente and Romo, 2005, 2006). In the monkey, the early activity of neurons in the primary somatosensory area S1 was identical on detected and undetected trials, but within 180 ms the activation expanded into parietal and medial frontal cortices (MFC) where it showed a large difference predictive of behavioral reports (high activation on detected trials and low activity on undetected trials, even for constant stimuli). In humans, a similar two-phase pattern was identified *within* area S1 (Jones et al., 2007). According to the authors, modeling of these S1 potentials required the postulation of a late top-down input from unknown distant areas to supragranular and granular layers, specific to detected stimuli. Thus, as in the visual modality (Del Cul et al., 2007; Supèr et al., 2001), tactile cortices may be mobilized into a conscious assembly only during a later phase of top-down amplification, synchronous to the activation of higher association cortices.

In the *auditory* modality, similarly, stimuli that are not consciously detected still trigger considerable sensory processing, including 40 Hz steady-state responses (Gutschalk et al., 2008) and mismatch negativities (MMN), i.e., electrophysiological responses that arise primarily from the temporal lobe in response to rare, deviant, or otherwise unpredictable auditory stimuli (Allen et al., 2000; Bekinschtein et al., 2009a; Diekhof et al., 2009; Näätänen, 1990). Once again, conscious and nonconscious stimuli differ in a late (>200 ms) and global P3 wave arising from bilateral prefronto-parietal generators, with joint enhancement of temporal auditory cortices (Bekinschtein et al., 2009a; Diekhof et al., 2009). These localizations are confirmed by an fMRI study that contrasted detected versus undetected near-threshold noise bursts (Sadaghiani et al., 2009) (Figure 1). Similarly, an fMRI study of speech listening at different levels of sedation showed partially preserved responses in temporal cortices but the total disappearance of activation in the left inferior frontal gyrus during deep sedation (Davis et al., 2007). A study by Hasson et al. (2007) further suggests that the content of what we consciously hear does not depend on early modality-specific responses in auditory cortex, but rather on late fronto-parietal cross-modal computations. Using the McGurk illusion (perception of a syllable "ta" when simultaneously hearing "pa" and seeing a face saying "ka"), they dissociated the objective auditory and visual stimuli from the subjective percept. Using fMRI repetition suppression, they then showed that early auditory cortices coded solely for the objective auditory stimulus, while the perceived subjective conscious content was reflected in the activation of the left posterior inferior frontal gyrus and anterior inferior parietal lobule. In this instance, at least, PFC activation could not be attributed to a generic process of attention, detection, or memory but demonstrably encoded the specific syllable perceived.

Turning to the *action* domain, several studies have demonstrated that the awareness of one's action, surprisingly, is not associated with primary or premotor cortices but arises from a higher-level representation of intentions and their expected sensory consequences; this representation involves prefrontal and parietal cortices, notably the angular gyrus (AG) (Desmurget et al., 2009; Farrer et al., 2008). Using direct cortical stimulation, Desmurget et al. (2009) observed a double dissociation: premotor stimulation often led to overt movements that the subject was not aware of performing, while angular gyrus stimulation led to a subjective perception of movement intention and performance even in the absence of any detectable muscle activation. In normal subjects, disrupted sensori-motor feedback has also been used to define a minimal contrast between subliminal versus conscious gestures. For instance, when a temporal delay or a spatial bias was introduced in the visual feedback provided to participants about their own hand movements, they continuously adjusted their behavior, but these motor adjustments were only perceived consciously when the disruption exceeded a certain threshold (Farrer et al., 2008; Slachevsky et al., 2001). fMRI revealed that this nonlinearity related to a bilateral distributed network involving AG and PFC cortices (Farrer et al., 2008).

Perhaps the clearest evidence for a two-stage process in action awareness comes from studies of *error awareness* (Nieuwenhuis et al., 2001). In an antisaccade paradigm, participants were instructed to move their eyes in the direction opposite to a visual target. This instruction generated frequent errors, where the eyes first moved toward the stimulus and then away from it. Many of these erroneous eye movements remained undetected. Remarkably, immediately after such undetected errors, a strong and early (~80 ms) ERP component called the error-related negativity arose from midline frontal cortices (anterior cingulate or pre-SMA). Only when the error was consciously detected was this early waveform amplified and followed by a massive P3-like waveform, which fMRI associated with the expansion of activation into a broader network including left inferior frontal/anterior insula activity (Klein et al., 2007).

Convergence with Studies of Inattention and Dual Tasks

The experiments reviewed so far considered primarily *subliminal* paradigms where access to conscious reportability was modulated by reducing the incoming sensory information. However,

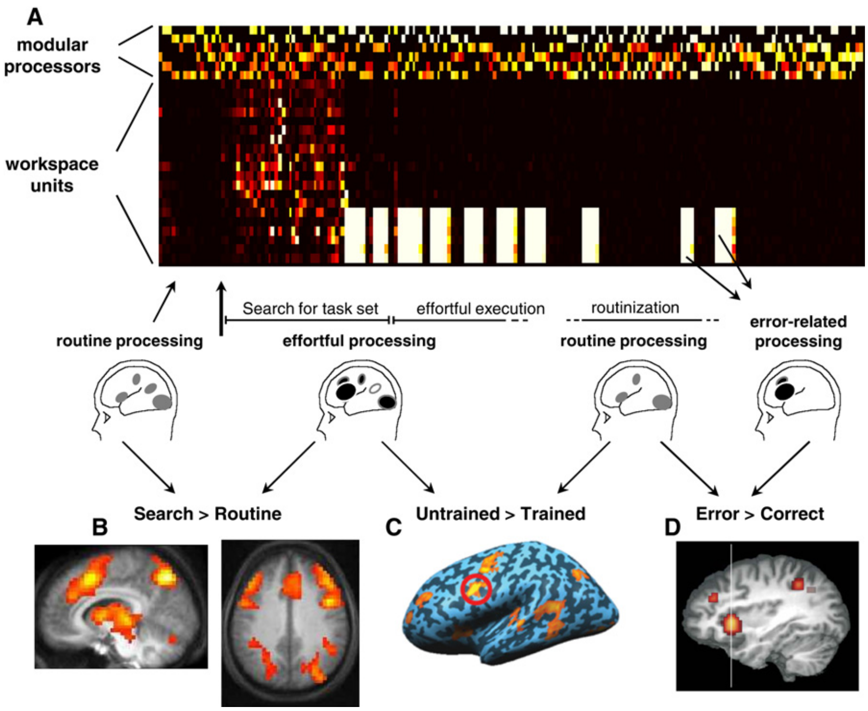

Figure 5. Recruitment of Global Fronto-Parietal Networks in Effortful Serial Tasks
(A) Simulations of the original global neuronal workspace proposal before, during, and after learning of an effortful Stroop-like task (adapted from Dehaene et al., 1998a). The figure shows the activity of various processor and workspace units as a function of time. Workspace units show strong activation (a) during the search for a task-appropriate configuration of workspace units; (b) during the effortful execution of a novel task (but not after its routinization); and (c) after errors, or whenever higher control is needed.
(B–D) Example of corresponding global fronto-parietal activations as seen with fMRI. (B) Strong activation of a distributed network involving PFC during effortful search for the solution of a "master-mind" type problem, with a sudden collapse as soon as a routine solution is found (adapted from Landmann et al., 2007). (C) Activation of inferior PFC during dual-task performance which diminishes with training (adapted from Dux et al., 2009). (D) Activation of a distribution parieto-prefrontal-cingulate network on error and conflict trials (adapted from the meta-analysis by Klein et al., 2007).

similar findings arise from *preconscious* paradigms where withdrawal of attentional selection is used to modulate conscious access (Dehaene et al., 2006), resulting in either failed (attentional blink, AB) or delayed (psychological refractory period or PRP) conscious access. In such states, initial visual processing, indexed by P1 and N1 waves, can be largely or even entirely unaffected (Sergent et al., 2005; Sigman and Dehaene, 2008; Vogel et al., 1998). However, only perceived stimuli exhibit an amplification of activation in task-related sensory areas (e.g., parahippocampal place area for pictures of places) as well as the unique emergence of lateral and midline prefrontal and parietal areas (see also Asplund et al., 2010; Marois et al., 2004; Slagter et al., 2010; Williams et al., 2008). Temporally resolved fMRI studies indicate that, during the dual-task bottleneck, PFC activity evoked by the second task is delayed (Dux et al., 2006; Sigman and Dehaene, 2008). With electrophysiology, the P3b waveform again appears as a major correlate of conscious processing that is both delayed during the PRP (Dell'acqua et al., 2005; Sigman and Dehaene, 2008) and absent during AB (Kranczioch et al., 2007; Sergent et al., 2005). Seen versus blinked trials are also distinguished by another marker, the synchronization of distant frontoparietal areas in the beta band (Gross et al., 2004).

William James (1890) noted how conscious attention and effort are required for the controlled execution of novel nonroutine sequential tasks but is no longer needed or even detrimental once routine sets in. Thus, the comparison of effortful versus automatic tasks provides another contrast that, although not quite as minimal as the previous ones, should at least provide signatures of conscious-level processing consistent with other paradigms. Indeed, a broad network including inferior and dorsolateral prefrontal, anterior cingulated, and lateral parietal and intraparietal components is activated whenever human subjects perform effortful single or dual tasks (Marois and Ivanoff, 2005), and its activation diminishes with training in parallel to the reduction in behavioral cost (Dux et al., 2009). Strikingly, it suddenly drops as soon as subjects move into a routine mode of task execution (Landmann et al., 2007; Procyk et al., 2000) (Figure 5). On the contrary, focal cortical regions associated with automatized processing of the relevant sensory or motor attributes remain invariant or may even increase their activation in the course of routinization (e.g., Sigman et al., 2005).

Broad fronto-parietal networks also figure prominently among the distributed networks of coactive areas that can be isolated during spontaneous brain activity in the absence of an explicit task goal (Beckmann et al., 2005; Fox et al., 2006; Greicius et al., 2003; Mantini et al., 2007; Vincent et al., 2008). How this activity relates to conscious processing remains debated, since it can still be observed, to some extent, during sleep (He et al., 2008), vegetative state (Boly et al., 2009), or sedation in both humans (Greicius et al., 2008) and monkeys (Vincent et al., 2007), though interestingly with reduced functional connectivity (Schrouff et al., 2011). To resolve this issue, a direct test consists in identifying participants with a given spontaneous activity pattern and asking them whether they were experiencing a particular conscious content (Christoff et al., 2009; Mason et al., 2007). Such studies reveal a tight correlation between default-mode network activity and self-reported "mind-wandering" into episodic memory and self-oriented thought. Smallwood et al. (2008) further demonstrated that, during such mind-wandering periods, the P3 wave evoked by external events is reduced. Overall, these findings indicate that spontaneous activity, like external goal-driven activity, invades large-scale fronto-parietal networks and impose a strong limitation on the processing of external events, with the same signature as the attentional blink.

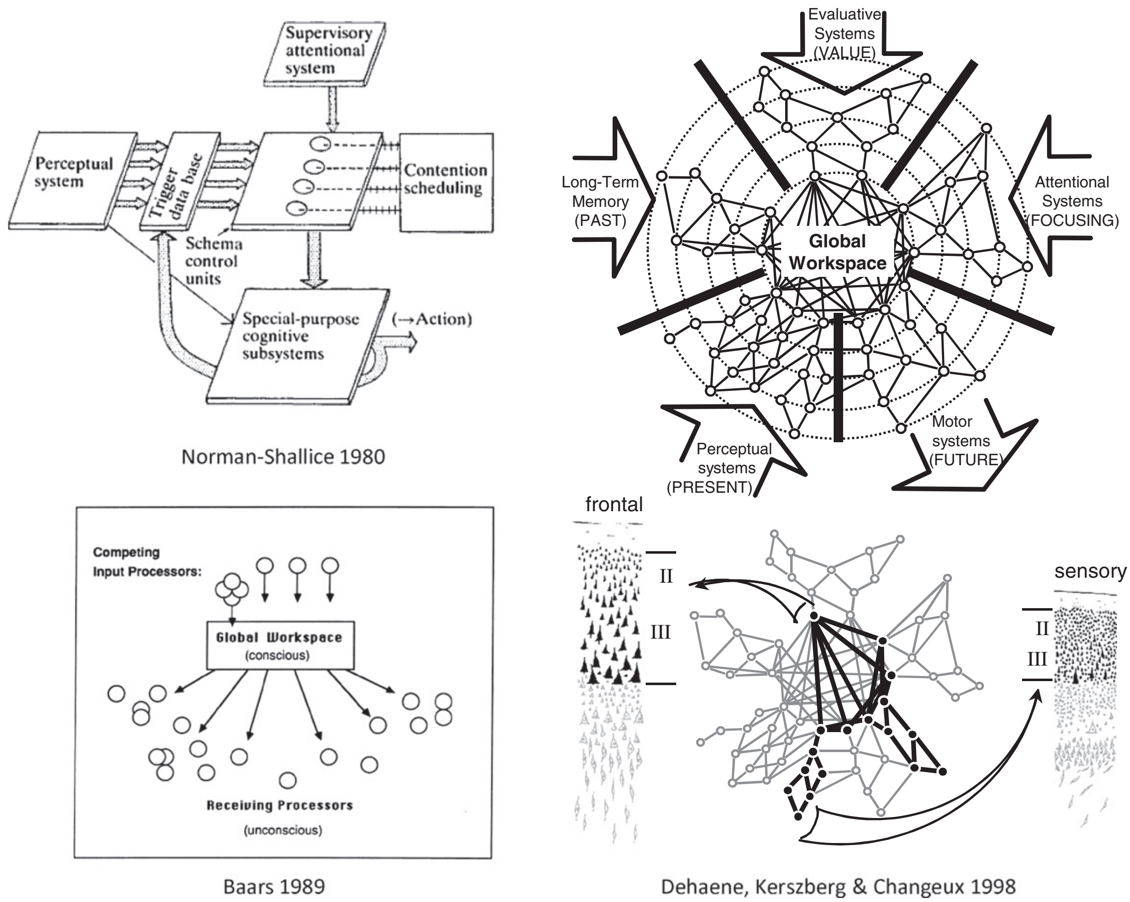

Figure 6. Historical Steps in the Development of Models of Conscious Processing
In the Norman and Shallice (1980) model (top left), conscious processing is involved in the supervisory attentional regulation, by prefrontal cortices, of lower-level sensori-motor chains. According to Baars (1989), conscious access occurs once information gains access to a global workspace (bottom left), which broadcasts it to many other processors. The global neuronal workspace (GNW) hypothesis (right) proposes that associative perceptual, motor, attention, memory, and value areas interconnect to form a higher-level unified space where information is broadly shared and broadcasted back to lower-level processors. The GNW is characterized by its massive connectivity, made possibly by thick layers II/III with large pyramidal cells sending long-distance cortico-cortical axons, particularly dense in prefrontal cortex (Dehaene et al., 1998a).

In conclusion, human neuroimaging methods and electrophysiological recordings during conscious access, under a broad variety of paradigms, consistently reveal a late amplification of relevant sensory activity, long-distance cortico-cortical synchronization at beta and gamma frequencies, and ''ignition'' of a large-scale prefronto-parietal network.

III. Theoretical Modeling of Conscious Access

The above experiments provide a convergent database of observations. In the present section, we examine which theoretical principles may account for these findings. We briefly survey the major theories of conscious processing, with the goal to try to isolate a core set of principles that are common to most theories and begin to make sense of existing observations. We then describe in more detail a specific theory, the Global Neuronal Workspace (GNW), whose simulations coarsely capture the contrasting physiological states underlying nonconscious versus conscious processing.

Convergence toward a Set of Core Concepts for Conscious Access

Although consciousness research includes wildly speculative proposals (Eccles, 1994; Jaynes, 1976; Penrose, 1990), research of the past decades has led to an increasing degree of convergence toward a set of concepts considered essential in most theories (for review, see Seth, 2007). Four such concepts can be isolated.

A supervision system. In the words of William James, ''consciousness'' appears as ''an organ added for the sake of steering a nervous system grown too complex to regulate itself'' (James, 1890, chapter 5). Posner (Posner and Rothbart, 1998; Posner and Snyder, 1975) and Shallice (Shallice, 1972, 1988; Norman and Shallice, 1980) first proposed that information is conscious when it is represented in an ''*executive attention*'' or ''*supervisory attentional*'' system that controls the activities of lower-level sensory-motor routines and is associated with prefrontal cortex (Figure 6). In other words, a chain of sensory, semantic, and motor processors can unfold without our awareness, as reviewed in the previous section, but conscious perception seems needed for the flexible control of their execution, such as their onset, termination, inhibition, repetition, or serial chaining.

A serial processing system. Descartes (1648) first observed that "ideas impede each other." Broadbent (1958) theorized conscious perception as involving access to a *limited-capacity channel* where processing is serial, one object at a time. The attentional blink and psychological refractory period effects indeed confirm that conscious processing of a first stimulus renders us temporarily unable to consciously perceive other stimuli presently shortly thereafter. Several psychological models now incorporate the idea that initial perceptual processing is parallel and nonconscious and that conscious access is serial and occurs at the level of a later *central bottleneck* (Pashler, 1994) or *second processing stage* of working memory consolidation (Chun and Potter, 1995).

A coherent assembly formed by re-entrant or top-down loops. In the context of the maintenance of invariant representations of the body/world through *reafference* (von Holst and Mittelstaedt, 1950), Edelman (1987) proposed *re-entry* as an essential component of the creation of a unified percept: the bidirectional exchange of signals across parallel cortical maps coding for different aspects of the same object. More recently, the dynamic core hypothesis (Tononi and Edelman, 1998) proposes that information encoded by a group of neurons is conscious only if it achieves not only *differentiation* (i.e., the isolation of one specific content out of a vast repertoire of potential internal representations) but also *integration* (i.e., the formation of a single, coherent, and unified representation, where the whole carries more information than each part alone). A notable feature of the dynamic core hypothesis is the proposal of a quantitative mathematical measure of *information integration* called Φ, high values of which are achieved only through a hierarchical recurrent connectivity and would be necessary and sufficient to sustain conscious experience: "consciousness is integrated information" (Tononi, 2008). This measure has been shown to be operative for some conscious/nonconscious distinctions such as anesthesia (e.g., Lee et al., 2009b; Schrouff et al., 2011), but it is computationally complicated and, as a result, has not yet been broadly applied to most of the minimal empirical contrasts reviewed above.

In related proposals, Crick and Koch (1995, 2003, 2005) suggested that conscious access involves forming a stable global *neural coalition*. They initially introduced reverberating gamma-band oscillations around 40 Hz as a crucial component, then proposed an essential role of connections to prefrontal cortex. Lamme and colleagues (Lamme and Roelfsema, 2000; Supèr et al., 2001) produced data strongly suggesting that *feedforward* or *bottom-up* processing alone is not sufficient for conscious access and that *top-down* or *feedback* signals forming *recurrent loops* are essential to conscious visual perception. Llinas and colleagues (Llinás et al., 1998; Llinás and Paré, 1991) have also argued that consciousness is fundamentally a thalamocortical closed-loop property in which the ability of cells to be intrinsically active plays a central role.

A global workspace for information sharing. The *theater metaphor* (Taine, 1870) compares consciousness to a narrow scene that allows a single actor to diffuse his message. This view has been criticized because, at face value, it implies a conscious homunculus watching the scene, thus leading to infinite regress (Dennett, 1991). However, capitalizing on the earlier concept of a *blackboard system* in artificial intelligence (a common data structure shared and updated by many specialized modules), Baars (1989) proposed a homunculus-free psychological model where the current conscious content is represented within a distinct mental space called *global workspace*, with the capacity to *broadcast* this information to a set of other processors (Figure 6). Anatomically, Baars speculated that the neural bases of his global workspace might comprise the "ascending reticular formation of the brain stem and midbrain, the outer shell of the thalamus and the set of neurons projecting upward diffusely from the thalamus to the cerebral cortex."

We introduced the Global Neuronal Workspace (GNW) model as an alternative cortical mechanism capable of integrating the supervision, limited-capacity, and re-entry properties (Changeux and Dehaene, 2008; Dehaene and Changeux, 2005; Dehaene et al., 1998a, 2003b, 2006; Dehaene and Naccache, 2001). Our proposal is that a subset of cortical pyramidal cells with long-range excitatory axons, particularly dense in prefrontal, cingulate, and parietal regions, together with the relevant thalamocortical loops, form a horizontal "neuronal workspace" interconnecting the multiple specialized, automatic, and nonconscious processors (Figure 6). A conscious content is assumed to be encoded by the sustained activity of a fraction of GNW neurons, the rest being inhibited. Through their numerous reciprocal connections, GNW neurons amplify and maintain a specific neural representation. The long-distance axons of GNW neurons then broadcast it to many other processors brain-wide. Global broadcasting allows information to be more efficiently processed (because it is no longer confined to a subset of nonconscious circuits but can be flexibly shared by many cortical processors) and to be verbally reported (because these processors include those involved in formulating verbal messages). Nonconscious stimuli can be quickly and efficiently processed along automatized or preinstructed processing routes before quickly decaying within a few seconds. By contrast, conscious stimuli would be distinguished by their lack of "encapsulation" in specialized processes and their flexible circulation to various processes of verbal report, evaluation, memory, planning, and intentional action, many seconds after their disappearance (Baars, 1989; Dehaene and Naccache, 2001). Dehaene and Naccache (2001) postulate that "this global availability of information (…) *is* what we subjectively experience as a conscious state."

Explicit Simulations of Conscious Ignition

The GNW has been implemented as explicit computer simulations of neural networks (Dehaene and Changeux, 2005; Dehaene et al., 1998a, 2003b; see also Zylberberg et al., 2009). These simulations incorporate spiking neurons and synapses with detailed membrane, ion channel, and receptor properties, organized into distinct cortical supragranular, granular, infragranular, and thalamic sectors with reasonable connectivity and temporal delays. Although the full GNW architecture was not simulated, four areas were selected and hierarchically interconnected (Figure 7). Bottom-up feed-forward connections linked each area to the next, while long-distance top-down

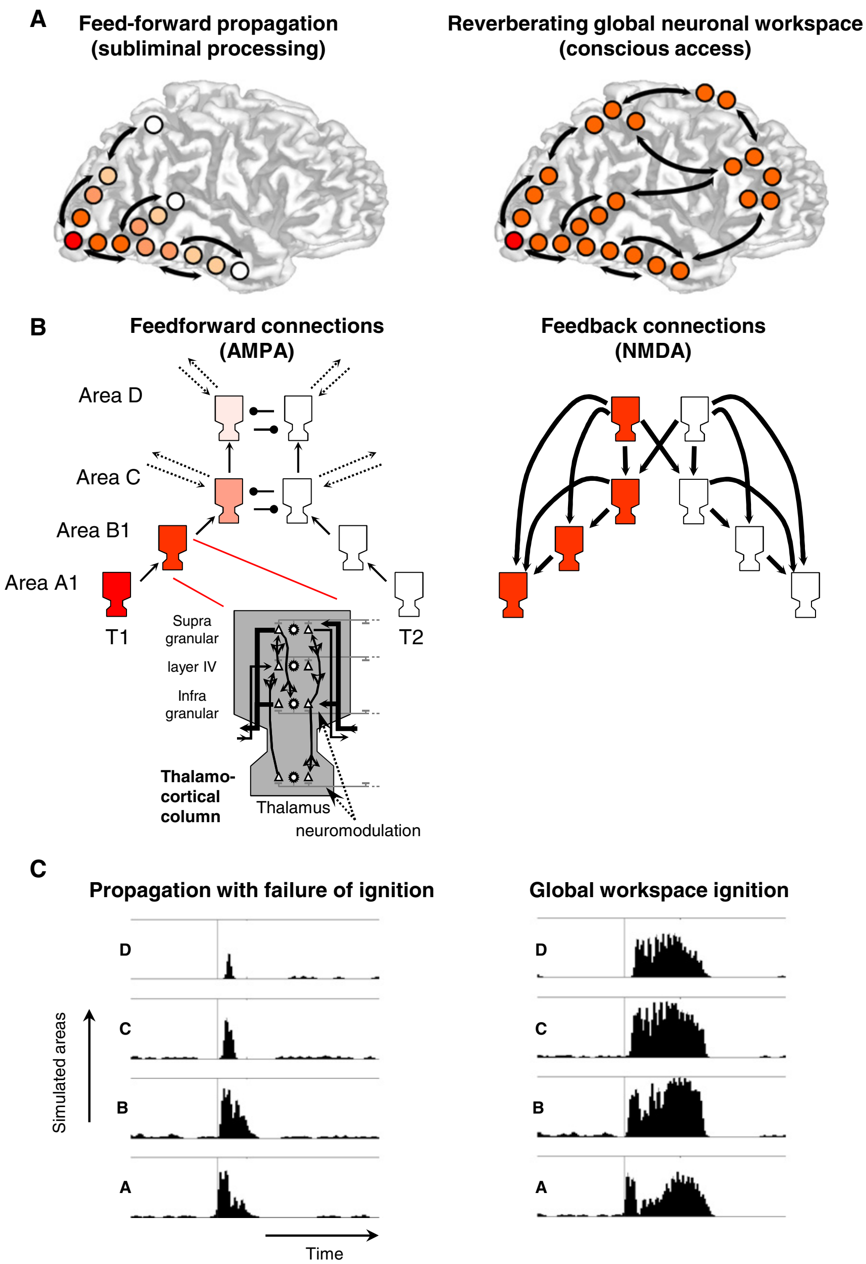

Figure 7. Schematic Representation of the Hypothesized Events Leading to Conscious Access According to the GNW Model

(A) Schema illustrating the main postulated differences between subliminal and conscious processing (adapted from Dehaene et al., 2006). During feed-forward propagation, sensory inputs progress through a hierarchy of sensory areas in a feedforward manner, successively contacting diverse and nonnecessarily compatible representations corresponding to all probabilistic interpretations of the stimuli. Multiple signals converge to support each other's interpretation in higher-level cortical areas. Higher areas feedback onto lower-level sensory representations, favoring a convergence toward a single coherent representation compatible with current goals. Such a self-connected system exhibits a dynamical threshold: if the incoming activity carries sufficient weight, it leads to the ignition of a self-supporting, reverberating, temporary, metastable, and distributed cell assembly that represents the current conscious contents and broadcasts it to virtually all distant sites.

(B) Architecture of an explicit neuronal simulation model of a small part of the GNW architecture (adapted from Dehaene and Changeux, 2005; Dehaene et al., 2003b). The model contains thalamic and cortical excitatory and inhibitory neurons, organized in layers with realistic interconnections (inset). Stimuli T1 and T2 can be presented at the lower level of a hierarchy of four successive areas, linked by feedforward (AMPA) nearest-neighbor connections and by global feedback (NMDA connections).

(C) Simulation of two single trials in which a identical pulse of brief stimulation was applied to sensory inputs for T1 (Dehaene and Changeux, 2005). Fluctuations in ongoing activity prevented ignition in the left diagram, resulting in a purely feedforward propagation dying out in higher-level areas. In the right diagram, the same stimulus crossed the threshold for ignition, resulting in self-amplification, a global state of activation, oscillation and synchrony, and a late long-lasting wave of late activation reaching back to early sensory areas.

connections projected to all preceding areas. Moreover, in a simplifying assumption, bottom-up connections impinged on glutamate AMPA receptors while the top-down ones, which are slower, more numerous, and more diffuse, primarily involved glutamate NMDA receptors (the plausibility of this hypothesis is discussed further below). In higher areas, inputs competed with each other through GABAergic inhibitory interneurons, and it was assumed (though not explicitly simulated) that the winning representation would be broadcasted by additional long-distance connections to yet other cortical regions.

Initial simulations explored the sequence of activity leading to conscious access. When sensory stimulation was simulated as a brief depolarizing current at the lowest thalamic level, activation propagated according to two successive phases (see Figure 7): (1) initially, a brief wave of excitation progressed into the simulated hierarchy through fast AMPA-mediated feedforward connections, with an amplitude and duration directly related to the initial input; (2) in a second stage, mediated by the slower NMDA-mediated feedback connections, the advancing feed-forward wave amplified its own inputs in a cascading manner, quickly leading the whole stimulus-relevant network into a global self-sustained reverberating or "ignited" state. This ignition was characterized by an increased power of local cortico-thalamic oscillations in the gamma band and their synchrony across areas (Dehaene et al., 2003b). This second phase of the simulation reproduces most of the empirical signatures of conscious access: late, all-or-none, cortically distributed potentials involving prefrontal cortex and other high-level associative cortices, with simultaneous increases in high-frequency power and synchrony (e.g., de Lafuente and Romo, 2006; Del Cul et al., 2007; Gaillard et al., 2009).

In GNW simulations, ignition manifests itself, at the cortical level, as a depolarization of layer II/III apical dendrites of pyramidal dendrites in a subset of activated GNW neurons defining the conscious contents, the rest being inhibited. In a geometrically accurate model of the pyramidal cell, the summed postsynaptic potentials evoked by long-distance signaling among these distributed sets of active cells would create slow intracellular currents traveling from the apical dendrites toward the cell's soma, summing up on the cortical surface as negative slow cortical potentials (SCPs) over regions coding for the conscious stimulus (see He and Raichle, 2009). Simultaneously, many other GNW neurons are strongly suppressed by lateral inhibition via GABAergic interneurons and define what the current conscious content is *not*. As already noted by Rockstroh et al. (1992, p. 175), assuming that many more neurons are inhibited than activated, "The surface positivity corresponding to these inhibited networks would then dominate over the relatively smaller spots of negativity caused by the reverberating excitation." Thus, the model can explain why, during conscious access, the resulting event-related potential is dominated by a positive waveform, the P3b. This view also predicts that scalp negativities should appear specifically over areas dense in neurons coding for the current conscious content. Indeed, in a spatial working memory task, all stimuli evoke a broad P3b, but when subtracting ERPs ipsilateral and controlateral to the side of the memorized items, negative potentials appeared over parietal cortex contralateral to the memorized locations (Vogel and Machizawa, 2004).

Further GNW simulations showed that ignition could fail to be triggered under specific conditions, thus leading to simulated nonconscious states. For very brief or low-amplitude stimuli, a feedforward wave was seen in the initial thalamic and cortical stages of the simulation, but it died out without triggering the late global activation, because it was not able to gather sufficient self-sustaining reverberant activation (Dehaene and Changeux, 2005). Even at higher stimulus amplitudes, the second global phase could also be disrupted if another incoming stimulus had been simultaneously accessed (Dehaene et al., 2003b). Such a disruption occurs because during ignition, the GNW is mobilized as a whole, some GNW neurons being active while the rest is actively inhibited, thus preventing multiple simultaneous ignitions. A strict seriality of conscious access and processing is therefore predicted and has been simulated (Dehaene and Changeux, 2005; Dehaene et al., 2003b; Zylberberg et al., 2010). Overall, these simulations capture the two main types of experimental conditions known to lead to nonconscious processing: subliminal states due to stimulus degradation (e.g., masking), and preconscious states due to distraction by a simultaneous task (e.g., attentional blink).

The transition to the ignited state can be described, in theoretical physics terms, as a stochastic phase transition—a sudden change in neuronal dynamics whose occurrence depends in part on stimulus characteristics and in part on spontaneous fluctuations in activity (Dehaene and Changeux, 2005; Dehaene et al., 2003b). In GNW simulations, prestimulus fluctuations in neural discharges only have a small effect on the early sensory stage, which largely reflects objective stimulus amplitude and duration, but they have a large influence on the second slower stage, which is characterized by NMDA-based reverberating integration and ultimately leads to a bimodal "all-or-none" distribution of activity, similar to empirical observations (Quiroga et al., 2008; Sergent et al., 2005; Sergent and Dehaene, 2004). Due to these fluctuations, across trials, the very same stimulus does or does not lead to global ignition, depending in part on the precise phase of the stimulus relative to ongoing spontaneous activity. This notion that prestimulus baseline fluctuations partially predict conscious perception is now backed up by considerable empirical data (e.g., Boly et al., 2007; Palva et al., 2005; Sadaghiani et al., 2009; Supèr et al., 2003; Wyart and Tallon-Baudry, 2009). More generally, these simulations provide a partial neural implementation of the psychophysical framework according to which conscious access corresponds to a "decision" based on the accumulation of stimulus-based evidence, prior knowledge, and biases (Dehaene, 2008; for specific implementations, see Lau, 2008, and the mathematical appendix in Del Cul et al., 2009).

Modeling Spontaneous Activity and Serial Goal-Driven Processing

An original feature of the GNW model, absent from many other formal neural network models, is the occurence of highly structured spontaneous activity (Dehaene and Changeux, 2005). Even in the absence of external inputs, the simulated GNW neurons are assumed to fire spontaneously, in a top-down manner, starting from the highest hierarchical levels of the simulation and propagating downward to form globally synchronized ignited states. When the ascending vigilance signal is large, several such spontaneous ignitions follow each other in a never-ending "stream" and can block ignition by incoming external stimuli (Dehaene and Changeux, 2005). These simulations capture some of the empirical observations on inattentional blindness (Mack and Rock, 1998) and mind wandering (Christoff et al., 2009; Mason et al., 2007; Smallwood et al., 2008). More complex network architectures have also been simulated in which a goal state is set and continuously shapes the structured patterns of activity that are spontaneously generated, until the goal is ultimately attained (Dehaene and Changeux, 1997; Zylberberg et al., 2010). In these simulations, ignited states are stable only for a transient time period and can be quickly destabilized by a negative reward signal that indicates deviation from the current goal, in which case they are spontaneously and randomly replaced by another discrete combination of workspace neurons. The dynamics of such networks is thus characterized by a constant flow of individual coherent episodes of variable duration, selected by reward signals in order to achieve a defined goal state. Architectures based on these notions have been applied to a variety of tasks (delayed response: Dehaene and Changeux, 1989; Wisconsin card sorting: Dehaene and Changeux, 1991; Tower of London: Dehaene and Changeux, 1997; Stroop: Dehaene et al., 1998a), although a single architecture common to all tasks is not yet in sight (but see Rougier et al., 2005). As illustrated in Figure 5, they provide a preliminary account of why GNW networks are spontaneously active, in a sustained manner, during effortful tasks that require series of conscious operations, including search, dual-task, and error processing.

In summary, we propose that a core set of theoretical concepts lie at the confluence of the diverse theories that have been proposed to account for conscious access: high-level supervision; serial processing; coherent stability through re-entrant loops; and global information availability. Furthermore, once implemented in the specific neuronal architecture of the GNW model, these concepts begin to provide a schematic account of the neurophysiological signatures that, empirically, distinguish conscious access from nonconscious processing. In particular, simulations of the GNW architecture can explain the close similarity of the brain activations seen during (1) conscious access to a single external stimulus; (2) effortful serial processing; and (3) spontaneous fluctuations in the absence of any stimulus or task.

IV. Present Experimental and Theoretical Challenges

The existing empirical data on conscious access still present many challenges for theorizing. Indeed, the above theoretical synthesis may still be refuted if some of its key neural components were found to be implausible or altogether absent in primate cerebral architecture, or if its predicted patterns of activity (the late "ignition") were found to be unnecessary, artifactual, noncoding, or noncausally related to conscious states. We consider each of these potential challenges in turn.

Connectivity and Architecture of Long-Distance Cortical Networks

Pyramidal neurons with long-distance axons. The main anatomical premise of the GNW model is that it consists of "a distributed set of cortical neurons characterized by their ability to receive from and send back to homologous neurons in other cortical areas horizontal projections through long-range excitatory axons mostly originating from the pyramidal cells of layers II and III" (Dehaene et al., 1998a) and more densely distributed in prefrontal and inferior parietal cortices. Do these units actually exist? The "special morphology" of the pyramidal cells from the cerebral cortex was already noted by Cajal (1899–1904), who mentioned their "long axons with multiple collaterals" and their "very numerous and complex dendrites." Von Economo (1929) further noted that these large pyramidal cells in layers III and V are especially abundant in areas "spread over the anterior two-thirds of the frontal lobe, (…) the superior parietal lobule" and "the cingulate cortex," among other cortical areas. Recent investigations have confirmed that long-distance cortico-cortical and callosal fibers primarily (though not exclusively) arise from layer II-III pyramids. Furthermore, quantitative analyses of the dendritic field morphology of layer III pyramidal neurons revealed a continuous increase of complexity of the basal dendrites from the occipital up to the prefrontal cortex within a given species (DeFelipe and Fariñas, 1992; Elston and Rosa, 1997, 1998) and from lower species (owl monkey, marmoset) up to humans (Elston, 2003). Layer IV PFC pyramidal neurons have as many as 16 times more spines in PFC than in V1 and, as a result, "the highly spinous cells in prefrontal areas may integrate many more inputs than cells in areas such as V1, TE, and 7a" (Elston, 2000). These observations confirm that PFC cells exhibit the morphological adaptations needed for massive long-distance communication, information integration, and broadcasting postulated in the GNW model and suggest that this architecture is particularly developed in the human species.

Global brain-scale white matter networks involving PFC. The GNW model further assumes that long-distance neurons form brain-scale networks involving prefrontal cortex as a key node. PFC indeed receives the most diverse set of corticocortical inputs from areas involved in processing all sensory modalities (Cavada et al., 2000; Fuster, 2008; Kringelbach and Rolls, 2004; Pandya and Yeterian, 1990; Petrides and Pandya, 2009). In the monkey cerebral cortex, long-range connections link, among others, the prefrontal cortex (area 46), the superior temporal sulcus, parietal area 7a, and the hippocampus together with the contralateral anterior and posterior cingulum, area 19, and the parahippocampal gyrus (Goldman-Rakic, 1988). In addition, areas within PFC are multiply interconnected (Barbas and Pandya, 1989; Preuss and Goldman-Rakic, 1991), and the superficial layers in PFC are characterized by an abundance of horizontal intrinsic axon projections that arise from supragranular pyramidal cells (Kritzer and Goldman-Rakic, 1995; Melchitzky et al., 1998, 2001; Pucak et al., 1996), thus exhibiting the massive and recurrent interconnectivity needed to sustain GNW ignition.

In humans, the course of cortical tracts can now be confirmed by diffusion tensor imaging (DTI) and tractography algorithms (Figure 8), yet with important limitations. Measurements typically average over relatively large voxels (a few millimeters aside) that contain a diversity of criss-crossing fibers. Even recent articles claiming to study the entire connectome (e.g., Hagmann et al., 2008) suffer for underestimation of the true long-distance connectivity of areas 46, 6, FEF, and LIP, critical to GNW theory and known from macaque invasive tracer studies and careful human anatomical dissections dating from the end of the 19th century (Dejerine, Meynert, Fleschig). In a still up-to-date volume, Dejerine (1895) distinguished five main tracts of long association fibers running deeply in the human white matter. Consistent with the GNW hypothesis, four of them connect prefrontal cortex with other cortical areas and are confirmed by diffusion tensor tractography (Catani and Thiebaut de Schotten, 2008) and by correlation of cortical thickness measures (Bassett et al., 2008; He et al., 2009). The networks thus identified converge well with those extracted by fMRI intercorrelation patterns during the resting state or by phase synchrony in the beta band during either working memory (Bassett et al., 2009) or attentional blink (Gross et al., 2004).

The importance of long-distance cortical projection pathways in conscious perception was recently tested in patients at the very first clinical stage of multiple sclerosis (MS), a neurological disease characterized by extensive white matter damage leading to perturbed long-distance connectivity (He et al., 2009; Reuter et al., 2007; Reuter et al., 2009). As predicted, MS patients showed abnormal conscious perception of masked stimuli: they needed a longer target-mask delay before conscious access occurred. Furthermore, this behavioral anomaly correlated with structural damage in the dorsolateral prefrontal white matter and the right occipito-frontal fasciculus (Figure 8). Importantly, subliminal priming was preserved.

While recent results thus support the existence of massive long-distance cortical networks involving PFC and their role in conscious perception, two points should be stressed. First, the PFC is increasingly being decomposed into multiple specialized and lateralized subnetworks (e.g., Koechlin et al., 2003; Voytek

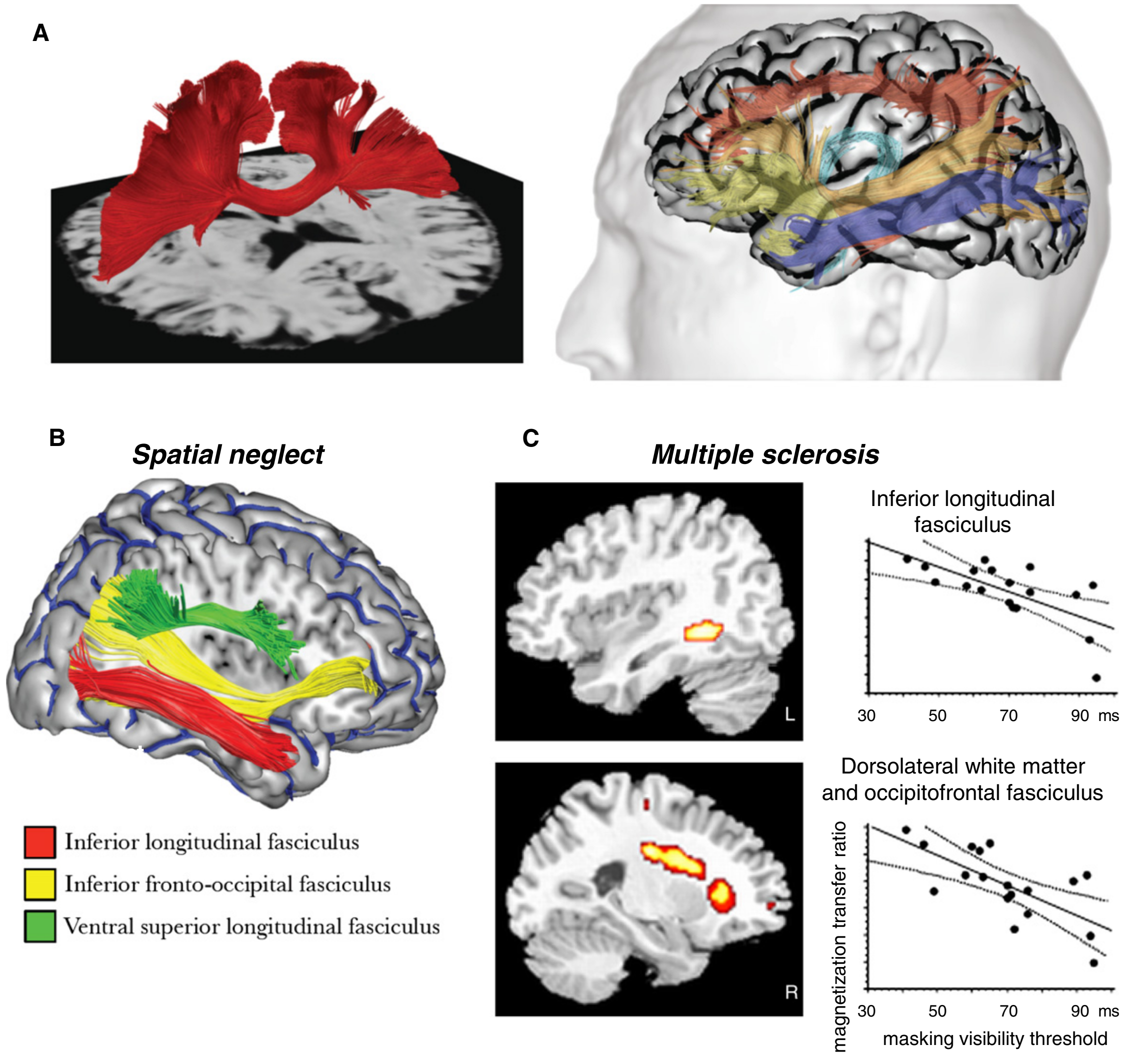

Figure 8. Role of Long-Distance Connections in Conscious Access

(A) Diffusion-based tracking of human brain connectivity reveals long-distance fiber tracts, both callosal (left) and intrahemispheric (right), forming an anatomical substrate for the proposed GNW (images courtesy of Michel Thiebaut de Schotten and Flavio Dell'Acqua).

(B and C) Pathologies of long-distance fiber tracts can be associated with deficits in conscious access. Spatial neglect patients (B) showing perturbed conscious processing of left-sided stimuli exhibit impaired right-hemispheric communication between occipital and parietal regions and frontal cortex along the inferior fronto-occipito fasciculus (IFOF), shown in yellow (image courtesy of Michel Thiebaut de Schotten; see Thiebaut de Schotten et al., 2005; Urbanski et al., 2008). Multiple sclerosis patients (C) in the very first stages of the disease exhibit impairments in the threshold for conscious detection of a masked visual target, correlating with impaired magnetization transfer, a measure of white matter integrity, in several long-distance fiber tracts (adapted from Reuter et al., 2009).

and Knight, 2010). These findings need not, however, be seen as contradicting the GNW hypothesis that these subnetworks, through their tight interconnections, interact so strongly as to make any information coded in one area quickly available to all others. Second, in addition to PFC, the nonspecific thalamic nuclei, the basal ganglia, and some cortical nodes are likely to contribute to global information broadcasting (Voytek and Knight, 2010). The precuneus, in particular, may also operate as a cortical "hub" with a massive degree of interconnectivity (Hagmann et al., 2008; Iturria-Medina et al., 2008). This region, plausibly homologous to the highly connected macaque posteromedial cortex (PMC) (Parvizi et al., 2006), is an aggregate of convergence-divergence zones (Meyer and Damasio, 2009) and is tightly connected to PFC area 46 and other workspace regions (Goldman-Rakic, 1999). In humans, the PMC may play a critical role in humans in self-referential processing (Cavanna and Trimble, 2006; Damasio, 1999; Vogt and Laureys, 2005), thus allowing any conscious content to be integrated into a subjective first-person perspective.

NMDA receptors and GNW simulations. GNW simulations assume that long-distance bottom-up connections primarily impinge on fast glutamate AMPA receptors while top-down ones primarily concern the slower glutamate NMDA receptor. This assumption contributes importantly to the temporal dynamics of the model, particularly the separation between a fast phasic bottom-up phase and a late sustained integration phase, mimicking experimental observations. It can be criticized as both receptor types are known to be present in variable proportions at glutamatergic synapses (for pioneering data on human receptor distribution, see Amunts et al., 2010). However, in agreement with the model, physiological recordings suggest that NMDA antagonists do not interfere with early bottom-up sensory activity, but only affect later integrative events such as the mismatch negativity in auditory cortex (Javitt et al., 1996). Thus, although GNW simulations adopted a highly simplified anatomical assumption of radically distinct distributions of NMDA and AMPA, which may have to be qualified in more realistic models, the notion that NMDA receptors contribute primarily to late, slow, and top-down integrative processes is plausible (for a related argument, see Wong and Wang, 2006).

Is Conscious Perception Slow and Late?

A strong statement of the proposed theoretical synthesis is that early bottom-up sensory events, prior to global ignition (<200–300 ms), contribute solely to nonconscious percept construction and do not systematically distinguish consciously seen from unseen stimuli. In apparent contradiction with this view, certain experiments, using both visual (Pins and Ffytche, 2003) or tactile stimuli (Palva et al., 2005), have observed that the early incoming wave of sensory-evoked activity (e.g., P1 component) is already enhanced on conscious compared to nonconscious trials. Lamme and collaborators (Fahrenfort et al., 2007) found amplification in visual cortex, just posterior to the P1 wave (110–140 ms). More frequently, at around 200–300 ms, surrounding the P2 ERP component, more negative voltages are reported over posterior cortices on visible compared to invisible trials (Del Cul et al., 2007; Fahrenfort et al., 2007; Koivisto et al., 2008, 2009; Railo and Koivisto, 2009; Sergent et al., 2005). Koivisto and collaborators have called this event the visual awareness negativity (VAN).

Several arguments, however, mitigate the possibility that these early or midlatency differences already reflect conscious perception. First, they may not be necessary and sufficient, as they are absent from several experiments (e.g., Lamy et al., 2009; van Aalderen-Smeets et al., 2006) (although one cannot exclude that they failed to be detected). Second, and most crucially, their profile of variation with stimulus variables such as target-mask delay does not always track the variations in subject's conscious reports (Del Cul et al., 2007; van Aalderen-Smeets et al., 2006). Third, they typically consist only in small modulations that ride on top of early sensory activations that are still strongly present on nonconscious trials (Del Cul et al., 2007; Fahrenfort et al., 2007; Sergent et al., 2005). Fourth, in this respect they resemble the small electrophysiological modulations that have been found to partially predict later perception even *prior* to the stimulus (e.g., Boly et al., 2007; Palva et al., 2005; Sadaghiani et al., 2009; Supèr et al., 2003; Wyart and Tallon-Baudry, 2009). The timing of these events makes it logically impossible that they already participate in the neural mechanism of conscious access. Similar, early differences in sensory activation between conscious and nonconscious trials may reflect fluctuations in prestimulus priors and in sensory evidence that contribute to subsequent conscious access, rather than be constitutive of a conscious state per se (Dehaene and Changeux, 2005; Wyart and Tallon-Baudry, 2009).

The evidence on this topic is still evolving, however, as a recent study found strong correlation of visibility with the P3b component when participants had no expectation of the stimuli, but a shift to the earlier P2 component when they already had a working memory representation of the target (Melloni et al., 2011). This study suggests that the timing of conscious access may vary with the experimental paradigm and that a Bayesian perspective, taking into account the subject's prior knowledge at multiple hierarchical cortical levels (Del Cul et al., 2009; Kiebel et al., 2008), may be an essential conceptual ingredient that still needs to be integrated to the above synthesis.

Whether it takes 200 ms, 300 ms, or even more, the slow and integrative nature of conscious perception is confirmed behaviorally by observations such as the ''rabbit illusion'' and its variants (Dennett, 1991; Geldard and Sherrick, 1972; Libet et al., 1983), where the way in which a stimulus is ultimately perceived is influenced by poststimulus events arising several hundreds of milliseconds after the original stimulus. Psychophysical paradigms that rely on quickly alternating stimuli confirm that conscious perception integrates over ~100 ms or more, while nonconscious perception is comparatively much faster (e.g., Forget et al., 2010; Vul and MacLeod, 2006).

Interestingly, recent research also suggests that spontaneous brain activity, as assessed by resting-state EEG recordings, may be similarly parsed into a stochastic series of slow ''microstates,'' stable for at least 100 ms, each exclusive of the other, and separated by sharp transitions (Lehmann and Koenig, 1997; Van de Ville et al., 2010). These microstates have recently been related to some of the fMRI resting-state networks (Britz et al., 2010). Crucially, they are predictive of the thought contents reported by participants when they are suddenly interrupted (Lehmann et al., 1998, 2010). Thus, whether externally induced or internally generated, the ''stream of consciousness'' may consist in a series of slow, global, and transiently stable cortical states (Changeux and Michel, 2004).

Can Nonconscious Stimuli Produce a Global Ignition?

Another pillar of the proposed theoretical synthesis is that global ignition is unique to conscious states. This view would be challenged if some nonconscious stimuli were found to reproducibly evoke intense PFC activations, P3b waves, or late and distributed patterns of brain-scale synchronization. Taking up this challenge, some studies have indeed reported small but significant activations of prefrontal regions and a P3-like wave evoked by infrequent nonconscious stimuli (Brázdil et al., 1998, 2001; Muller-Gass et al., 2007; Salisbury et al., 1992). However, this wave is usually a novelty P3a response, with a sharp midline anterior positivity suggesting focal anterior midline generators, rather than the global P3 or ''late positive complex'' response evoked by novel stimuli. Similarly, van Gaal et al. (2011) used fMRI to examine which areas contributed to subliminal versus conscious processing of ''no-go'' signals—rare visual cues that instructed subjects to refrain from responding on this particular trial. Their initial observations suggested, provocatively, that subliminal no-go signals evoked prefrontal potentials corresponding to nonconscious executive processing (van Gaal et al., 2008). Subsequent fMRI, however, indicated that the generators of the subliminal response inhibition effect were restricted to a small set of specialized processors in midline preSMA and the junction of the bilateral anterior insula with the inferior frontal gyrus. Only conscious no-go signals triggered a broad and more anterior activation expanding into anterior cingulate, inferior, and middle frontal gyrus, dorsolateral prefrontal cortex, and inferior parietal cortex—a network fully compatible with the GNW model (see Figure 1).

Identifying the limits of nonconscious processing remains an active area of research, as new techniques for presentation of nonconscious stimuli are constantly appearing (e.g., Arnold et al., 2008; Wilke et al., 2003). A recent masking study observed that subliminal task-switching cues evoked detectable activations in premotor, prefrontal, and temporal cortices (Lau and Passingham, 2007), but with a much reduced amplitude compared to conscious cues. Another more challenging study (Diaz and McCarthy, 2007) reported a large network of cortical perisylvian regions (inferior frontal, inferior temporal, and angular gyrus) activated by subliminal words relative to subliminal pseudowords, and surprisingly more extended than in previous reports (e.g., Dehaene et al., 2001). Attentional blink studies also suggest that unseen words may cause surprisingly long-lasting ERP components (N400) (see also Gaillard et al., 2007; Vogel et al., 1998). A crucial question for future research is whether these activations remain confined to specialized subcircuits, for instance in the left temporal lobe (Sergent et al., 2005), or whether they constitute true instances of global cortical processing without consciousness.

Do Prefrontal and Parietal Networks Play a Causal Role in Conscious Access?

Brain imaging is only correlational in nature, and leaves open the possibility that distributed ignition involving PFC is a mere epiphenomenon or a consequence of conscious access, rather than being one of its necessary causes. Causality is a demanding concept that can only be assessed by systematic lesion or interference methods, which are of very limited applicability in human subjects. Nevertheless, one prediction of the GNW model is testable: lesioning or interfering with prefrontal or parietal cortex activity, at sites quite distant from visual areas, should disrupt conscious vision. This prediction was initially judged as so counterintuitive as to be immediately refuted by clinical observations, because frontal lobe patients do not appear to be unconscious (Pollen, 1999). However, recent evidence actually supports the GNW account. In normal subjects, transcranial magnetic stimulation (TMS) over either parietal or prefrontal cortex can prevent conscious perception and even trigger a sudden subjective disappearance of visual stimulis during prolonged fixation (Kanai et al., 2008), change blindness (Beck et al., 2006), binocularly rivalry (Carmel et al., 2010), inattentional blindness (Babiloni et al., 2007), and attentional blink paradigms (Kihara et al., 2011). Over prefrontal cortex, bilateral theta-burst TMS leads to a reduction of subjective visibility with preserved objective sensori-motor performance (Rounis et al., 2010). We recently made similar observations in patients with focal prefrontal lesions (Del Cul et al., 2009): their masking threshold was significantly elevated, in tight correlation with the degree of expansion of the lesions into left anterior prefrontal cortex, while subliminal performance on "not-seen" trials did not differ from normal. In more severe and diffuse cases, following traumatic brain injury, bilateral lesions of fronto-parietal cortices or, characteristically, of the underlying white matter, can cause coma or vegetative state (Tshibanda et al., 2009). Frontal-lobe patients also suffer from impaired conscious processing, in such syndromes as hemineglect, abulia, akinetic mutism, anosognosia, or impaired autonoetic memory, while they frequently exhibit preserved or even heightened capacity for automatic action as indexed by utilization and imitation behaviors (Husain and Kennard, 1996; Lhermitte, 1983; Passingham, 1993). Indeed, spatial hemineglect, in which conscious access fails for stimuli contralateral to the lesion, can arise from focal frontal lesions as well as from impairments of the long-distance fiber tracts linking posterior visual areas with the frontal lobe (Bartolomeo et al., 2007; He et al., 2007; Thiebaut de Schotten et al., 2005; Urbanski et al., 2008) (Figure 8).

While suggestive, these observations do not quite suffice to establish that a frontal contribution is causally necessary for conscious perception. Arguably, the above effects may not necessarily indicate a direct or central contribution of PFC to conscious access, but rather could be mediated by another brain structure under the influence of PFC or parietal networks, such as the thalamic nuclei. Also, it is difficult to exclude a contribution of reduced top-down attention or enhanced distractibility in frontal patients or TMS subjects—although some studies have attempted to control for these factors by equalizing primary task performance (Rounis et al., 2010) or by demonstrating a preserved capacity for attentional modulation (Del Cul et al., 2009). Ultimately, the crucial experiment would involve inducing a change in the actual conscious *content*, rather than a mere elevation of the reportability threshold, by stimulating PFC or other components of the GNW networks. While we know of no such experiment yet, microstimulation and optogenetic methods now make it feasible, at least in nonhuman animals.

Does the Theory Lead to Clinical Applications?

A strong test for any theory of consciousness is whether it can be clinically used. Conscious access is altered or reduced in three clinicial situations: schizophrenia, anesthesia, and loss of consciousness due to coma or vegetative state. Can the proposed theoretical synthesis shed some light on these issues?

Schizophrenia. Friston and Frith (1995) first hypothesized that schizophrenia results from a functional disconnection of long-distance prefrontal cortex projection affecting primarily the strength of N-methyl-D-aspartate receptor (NMDAR)-mediated synaptic transmission (Niswender and Conn, 2010; see also Roopun et al., 2008; Stephan et al., 2009). Bullmore et al. (1997) further suggested a disruption of anatomical connectivity possibly associated with an aberrant synaptic elimination during late adolescence and early adulthood (Changeux and Danchin, 1976; McGlashan and Hoffman, 2000), a possibility consistent with the fact that many potential risk genes are involved in neuronal and connectivity development (Karlsgodt et al., 2008). The volume or density of white matter tracks is, indeed, reduced in a number of regions, including the temporal and prefrontal lobes, the anterior limb of the internal capsule, and the cingulum bundle (Lynall et al., 2010; Oh et al., 2009). The cingulate fasciculus disconnection would, secondarily, impair the link to reward and emotional systems (Holland and Gallagher, 2004), thus possibly accounting for the known effect of dopaminergic neuroleptics.

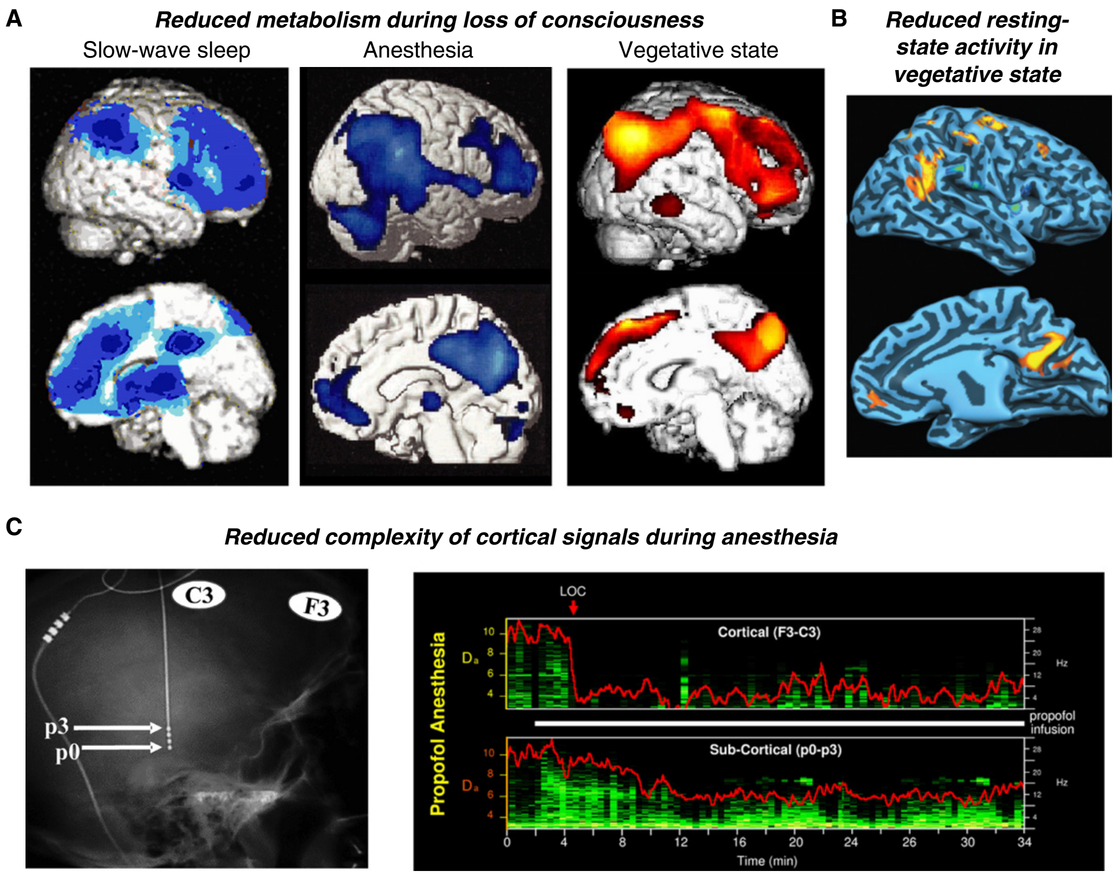

Figure 9. Cortical Measures of Loss of Consciousness in Sleep, Anesthesia, and Vegetative State
(A) Massive drops in cortical metabolism observed with PET rCBF measurements in slow-wave sleep (Maquet et al., 1997), anesthesia (Kaisti et al., 2002), and vegetative state (Laureys et al., 2004).
(B) Reduced activity in a "resting-state" distributed cortical network in three vegetative state patients, as measured by independent component analysis of fMRI data (adapted from Cauda et al., 2009).
(C) Sudden change in dimensional activation, a nonlinear dynamics measure of EEG complexity, at the precise point of loss of consciousness during anesthesia (adapted from Velly et al., 2007). Signals were measured from the scalp as well as from the thalamus using depth electrodes (left). Only the scalp (cortical) EEG showed a dramatic and discontinuous change accompanying loss of consciousness (right).

Schizophrenia thus provides another possible test of the hypothesis that disruption of PFC long-distance connections impairs conscious access. Indeed, there is direct evidence for impaired neural signatures of conscious access, together with normal subliminal processing, in schizophrenic patients (Dehaene et al., 2003a; Del Cul et al., 2006; Luck et al., 2006). As in frontal patients, the threshold for conscious access to masked visual stimuli is elevated in schizophrenia (Del Cul et al., 2006). The P3b wave is typically delayed and reduced in amplitude, in both chronic and first-episode schizophrenics (Demiralp et al., 2002; van der Stelt et al., 2004) and their siblings (Groom et al., 2008). Frontal slow waves associated with working memory are similarly impaired (Kayser et al., 2006). Gamma- and beta-band power and long-distance phase synchrony are drastically reduced, even during simple perceptual tasks (Uhlhaas et al., 2006; Uhlhaas and Singer, 2006). By applying graph-theoretical tools to MEG recordings, Bassett et al. (2009) observed that activation in the beta and gamma bands failed to organize into long-distance parieto-frontal networks that were "cost-efficient," i.e., had close to the minimal number of connections needed to confer a high efficiency of information transmission. In summary, the neuronal processes of conscious access appear systematically deteriorated in schizophrenia.

Anesthesia. A classical question concerns whether general anesthetics alter consciousness by binding to molecular target sites, principally ion channels and ligand-gated ion channels (Forman and Miller, 2011; Li et al., 2010; Nury et al., 2011) present all over the cortex, in specific and nonspecific thalamic nuclei, or, as suggested by intracerebral microinjections (Sukhotinsky et al., 2007), localized to specific sets of brain stem neurons (for review, see Alkire et al., 2008; Franks, 2008). Anesthetic-induced loss of consciousness usually coincides with the disruption of activity in extensive regions of cerebral cortex, particularly the precuneus, posterior cingulate cortex, cuneus, localized regions of the lateral frontal and parietal cortices, and occasionally the cerebellum (Franks, 2008; Kaisti et al., 2002; Schrouff et al., 2011; Veselis et al., 2004) (Figure 9). Consistent with these views, Velly et al. (2007) found that during induction of anesthesia by sevofurane and propofol in human patients with Parkinson disease, cortical EEG complexity decreased dramatically at the precise time where consciousness was lost, while for several minutes there was little change in subcortical signals, and eventually a slow decline (Figure 9). These data suggest that in humans, the early stage of anesthesia correlates with cortical disruption, and that the effects on the thalamus are indirectly driven by cortical feedback (Alkire et al., 2008). Indeed, in the course of anesthesia induction, there is a decrease in EEG coherence in the 20 to 80 Hz frequency range between right and left frontal cortices and between frontal and occipital territories (John and Prichep, 2005). Quantitative analysis of EEG under propofol induction further indicates a reduction of mean information integration, as measured by Tononi's Phi measure, around the γ-band (40 Hz) and a breakdown of the spatiotemporal organization of this particular band (Lee et al., 2009b). In agreement with experiments carried out with rats (Imas et al., 2005; Imas et al., 2006), quantitative EEG analysis in humans under propofol anesthesia induction noted a decrease of directed feedback connectivity with loss of consciousness and a return with responsiveness to verbal command (Lee et al., 2009a). Also, during anesthesia induced by the benzodiazepine midazolam, an externally induced transcranial pulse evoked reliable initial activity monitored by ERPs in humans, but the subsequent late phase of propagation to distributed areas was abolished (Ferrarelli et al., 2010). These observations are consistent with the postulated role of top-down frontal-posterior amplification in conscious access (see also Supèr et al., 2001).

Coma and vegetative state. The clinical distinctions between coma, vegetative state (Laureys, 2005), and minimal consciousness (Giacino, 2005) remain poorly defined, and even fully conscious but paralyzed patients with *locked-in syndrome* can remain undetected. It is therefore of interest to see whether objective neural measures and GNW theory can help discriminate them. In coma and vegetative state, as with general anesthesia, global metabolic activity typically decreases to ~50% of normal levels (Laureys, 2005). This decrease is not homogeneous, however, but particularly pronounced in GNW areas including lateral and mesial prefrontal and inferior parietal cortices (Figure 9). Spontaneous recovery from VS is accompanied by a functional restoration of this broad frontoparietal network (Laureys et al., 1999) and some of its cortico-thalamo-cortical connections (Laureys et al., 2000; see also Voss et al., 2006).

Anatomically, prediction of recovery from coma relies on the comprehensive assessment of all structures involved in arousal and awareness functions, namely, the ascending reticular activating system located in the postero-superior part of the brainstem and structures encompassing thalamus, basal forebrain, and fronto-parietal association cortices (Tshibanda et al., 2009). Lesion or inhibition of part of this system suffices to cause immediate coma (e.g., Parvizi and Damasio, 2003). Studies on traumatic coma patients with conventional MRI showed that lesions of the pons, midbrain, and basal ganglia were predictive of poor outcome especially when they were bilateral (Tshibanda et al., 2009). In relation with the GNW model, it is noteworthy that prediction of nonrecovery after 1 year could be calculated with up to 86% sensitivity and 97% specificity when taking into account both diffusion tensor and spectroscopic measures of cortical white matter integrity (Tshibanda et al., 2009).

The objective neural measures of conscious processing demonstrated earlier in this review should be applicable to the difficult clinical problem of detecting consciousness in noncommunicating patients. Using fMRI, a few patients initially classified as vegetative by clinical signs showed essentially normal activations of distributed long-distance cortical networks during speech processing and mental imagery tasks (Owen et al., 2006; Monti et al., 2010), and one patient proved able to voluntarily control them to provide yes/no answers to simple personal questions, clearly indicating some degree of preserved conscious processing (Monti et al., 2010). In an effort to isolate a more theoretically validated scalp signature of conscious sensory processing, Bekinschtein et al. (2009a) recorded ERPs to local versus global violations of an auditory regularity. When hearing a deviant tone after a sequence of repeated standard tones (sequence XXXXY), a local mismatch response was elicited nonconsciously even in coma and vegetative-state patients, as previously demonstrated (e.g., Fischer et al., 2004). However, when this sequence XXXXY was repeatedly presented, such that the final tone change could be expected, the presentation of a deviant monotonic sequence (XXXXX) engendered a P3b wave in normal subjects that was absent in coma patients and in most vegetative-state patients but could still be observed in minimally conscious and locked-in patients. This paradigm, founded upon previous identification of the P3b component as a signature of conscious processing, is now undergoing validation as a means of identifying residual conscious processing in patients (Faugeras et al., 2011).

V. Conclusion and Future Research Directions

The present review was deliberately limited to conscious access. Several authors argue, however, for additional, higher-order concepts of consciousness. For Damasio and Meyer (2009), *core consciousness* of incoming sensory information requires integrating it with a sense of *self* (the specific subjective point of view of the perceiving organism) to form a representation of how the organism is modified by the information; *extended consciousness* occurs when this representation is additionally related to the memorized past and anticipated future (see also Edelman, 1989). For Rosenthal (2004), a *higher-order thought*, coding for the very fact that the organism is currently representing a piece of information, is needed for that information to be conscious. Indeed, *metacognition*, or the ability to reflect upon thoughts and draw judgements upon them, is often proposed as a crucial ingredient of consciousness (Cleeremans et al., 2007; Lau, 2008) (although see Kanai et al., 2010, for evidence that metacognitive judgements can occur without conscious perception). In humans, as opposed to other animals, consciousness may also involve the construction of a *verbal narrative* of the reasons for our behavior (Gazzaniga et al., 1977). Although this narrative can be fictitious (Wegner, 2003), it would be indispensable to interindividual communication (Bahrami et al., 2010; Frith, 2007).

Metacognition and self-representation have only recently begun to be studied behaviorally with paradigms simple enough to extend to nonhuman species (Kiani and Shadlen, 2009; Terrace and Son, 2009) and to be related to specific brain measurements, notably anterior prefrontal cortex (Fleming et al., 2010). Thus, our view is that these concepts, although essential, have not yet received a sufficient empirical and neurophysiological definition to figure in this review. Following Crick and Koch (1990), we focused solely here on the simpler and well-studied question of what neurophysiological mechanisms differentiate conscious access to some information from nonconscious processing of the same information. Additional work will be needed to explore, in the future, these important aspects of higher-order consciousness.

In the present state of investigations, experimental measures of conscious access identified in this review include: (1) sudden, all-or-none ignition of prefronto-parietal networks; (2) concomitant all-or-none amplification of sensory activation; (3) a late global P3b wave in event-related potentials; (4) late amplification of broad-band power in the gamma range; (5) enhanced long-distance phase synchronization, particularly in the beta range; and (6) enhanced causal relations between distant areas, including a significant top-down component. Many of these measures are also found during complex serial computations and in spontaneous thought. There is evidence that they rely on an anatomical network of long-distance connections that is particularly developed in the human brain. Finally, pathologies of these networks or their long-distance connections are associated with impairments of conscious access.

In the future, as argued by Haynes (2009), the mapping of conscious experiences onto neural states will ultimately require not only a neural distinction between seen and not-seen trials, but also a proof that the proposed conscious neural state actually encodes all the details of the participant's current subjective experience. Criteria for a genuine one-to-one mapping should include verifying that the proposed neural state has the same perceptual stability (for instance over successive eye movements) and suffers from the same occasional illusions as the subject's own report. Multivariate decoding techniques provide pertinent tools to address this question and have already been used to infer conscious mental images from early visual areas (Haynes and Rees, 2005; Thirion et al., 2006) and from inferotemporal cortex (Schurger et al., 2010; Sterzer et al., 2008). However, decoding the more intermingled neural patterns expected from PFC and other associative cortices is clearly a challenge for future research (though see Fuentemilla et al., 2010).

Another important question concerns the genetic mechanisms that, in the coure of biological evolution, have led to the development of the GNW architecture, particularly the relative expansion of PFC, higher associative cortices, and their underlying long-distance white matter tracts in the course of hominization (see Avants et al., 2006; Schoenemann et al., 2005; Semendeferi et al., 2002). Finally, now that measures of conscious processing have been identified in human adults, it should become possible to ask how they transpose to lower animal species (Changeux, 2006, 2010) and to human infants and fetuses (Dehaene-Lambertz et al., 2002; Gelskov and Kouider, 2010; Lagercrantz and Changeux, 2009), in whom genuine but immature long-distance networks have been described (Fair et al., 2009; Fransson et al., 2007).

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