



Social Semantics: The role of conceptual knowledge and cognitive control in a neurobiological model of the social brain

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ABSTRACT

Research in social neuroscience has primarily focused on carving up cognition into distinct pieces, as a function of mental process, neural network or social behaviour, while the need for unifying models that span multiple social phenomena has been relatively neglected. Here we present a novel framework that treats social cognition as a case of semantic cognition, and which is neurobiologically constrained and generalizable, with clear, testable predictions regarding sociocognitive processing in the context of both health and disease. According to this framework, social cognition relies on two principal systems of representation and control. These systems are neuroanatomically and functionally distinct, but interact to (1) enable development of foundational, conceptual-level knowledge and (2) regulate access to this information in order to generate flexible and context-appropriate social behaviour. The Social Semantics framework shines new light on the mechanisms of social information processing by maintaining as much explanatory power as prior models of social cognition, whilst remaining simpler, by virtue of relying on fewer components that are “tuned” towards social interactions.

1. Introduction

The neuroscientific study of social cognition and social behaviours is now undoubtedly one of the most rapidly developing domains of systems neuroscience, and in recent years, its influence has spread to have impact upon fields ranging from psychiatry to behavioural economics (Adolphs, 2009; Cacioppo and Berntson, 1992; Cacioppo and Decety, 2011; Frith and Frith, 2011; Lieberman, 2006). Like any developing research programme, sub-fields within social neuroscience have emerged, which specialise in perceptual, cognitive, emotional and regulatory functions and their associated neural substrates (Adolphs, 2010). Further, within each of these sub-fields, an increasing number of distinct phenomena are being identified as worthy of investigation. Indeed, as is the case with psychology and neuroscience more generally, the dominant approach has been to carve up social cognition into distinct pieces, as a function of mental process, neural network or social behaviour.

The focus on compartmentalising social cognition according to a range of distinct organising principles has made a valuable contribution to understanding the cognitive and neural bases of social cognition. At the same time, the need for unifying models that span multiple social phenomena, and offer a generalizable framework (Adolphs, 2010), has

been relatively neglected. We argue that progress on key questions in social neuroscience will be optimised if broader frameworks for considering cognition in general are considered together with developments made in sub-fields of social cognition. Therefore, the aim of the present paper is to show how a parallel line of literature, which is usually considered more relevant to the cognitive neuroscience of language and object knowledge, has established foundational principles that can inform social neuroscience theory. In fact, we will argue that upon closer inspection, the two seemingly distinct domains appear to dovetail in terms of the processes they describe and the brain regions they implicate. As such, by taking inspiration from the semantic cognition literature, the current paper is able to offer an exciting new direction for social neuroscience theory, which is predicated on a wealth of evidence and offers a point of departure from existing approaches to understanding the social brain.

One of cognitive neuroscience's most successful theoretical perspectives in recent years is the controlled semantic cognition (CSC) framework (Lambon Ralph et al., 2016). The proponents of CSC use the term ‘semantic cognition’ to describe a set of supramodal processes that underpin how meaning is gathered from the environment. These processes include the distillation of verbal and non-verbal experiences to form a coherent knowledge base of the meaning of words, objects,

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people and events. Moreover, this foundation of conceptual knowledge is regulated by a supervisory system that supports interactions with our environment (including other agents within it) to occur in a flexible manner, as well as in a controlled, and context-appropriate manner.

Whilst the term ‘semantics’ is more frequently associated with language abilities, according to the CSC framework, a central semantic system is key not only to comprehension and production of verbal behaviours, but also to nonverbal behaviours including action perception (Caspers et al., 2010; Davey et al., 2015), object interactions (Bar, 2004; Corbett et al., 2009; Culham and Valyear, 2006), and a range of socio-cognitive processes, including person identification (Kanwisher, 2010; Rice et al., 2018b), empathy, and emotion recognition (Adolphs, 2002; Binney et al., 2016a; Singer and Lamm, 2009). The predictions of the framework are supported by over a decade’s worth of multi-method research, and its great appeal lies in the fact in that it offers both a relatively straight-forward computational model with clear neurobiological constraints, as well as clinically-relevant hypotheses.

In the current paper, we outline how the CSC framework can be broadly transposed into the domain of social cognition. Going even further, we propose that it is constructive to describe social cognition as a case of semantic cognition, which means we expect it to operate under the same basic principles (i.e., a bipartite distinction between representation and control processes). As such, in the following sections, we first describe the key components of the CSC framework, and then briefly review some existing research that has begun to link it to the neurobiology of socio-affective behaviour. Second, we propose some modifications of the CSC framework that explicitly link it to social phenomena, and then compare it with other models of social cognition, highlighting key distinctions, relative strengths and possible weaknesses. Finally, we consider how operationalising social cognition under a modified CSC framework can guide and inform a range of future research avenues. The impact on future research includes understanding the neurocognitive mechanisms that underpin social interactions, as well as the emergence and development of these systems, and the biological underpinnings of clinical conditions whose symptoms are typified by disordered social information processing (e.g., autism spectrum conditions and schizophrenia).

2. Basic principles of the CSC framework

The CSC framework has two principal neural systems. The first is *representational* in nature, and supports the acquisition and long-term storage of conceptual knowledge (Fig. 1A). The second system is responsible for *control* processes that manipulate semantic information and utilise this information in line with task- and context-specific requirements (Fig. 1B). As we discuss below, a growing body of multi-method evidence supports claims for the existence of these two distinct but interacting semantic sub-systems (Lambon Ralph et al., 2016).

The CSC framework characterises the semantic representational system as having a hub-and-spoke architecture (Fig. 1A). This refers to the idea that modality-specific systems distributed across the brain (the ‘spokes’) play an essential role in supplying the information required to establish concepts, namely our multimodal sensorimotor, linguistic, and affective experiences of concept exemplars. This notion of ‘embodiment’ is shared among a number of contemporary neurobiological accounts of semantic memory (e.g., Martin, 2006). However, the CSC framework is fundamentally different to prior embodied accounts, in that it argues for the necessity of an additional, supramodal hub. The supramodal hub serves two functions: 1) it mediates transmodal interactions between different modes of input from the ‘spokes’ and 2) it encodes a deeper level of representation that abstracts beyond a linear combination of such inputs from the ‘spokes’. This deeper and more abstract level of representation is argued to be critical for the production of generalizable concepts. Moreover, whilst the supposition of an existence of multiple transmodal ‘convergence zones’ appears within other accounts of higher-order cognition (e.g., Damasio et al., 1996),

the claim that a central semantic hub is responsible for encoding all types of concepts (including knowledge of concrete objects and more abstract conceptual constructs) is the hallmark feature of the CSC framework. In particular, it holds that this principal hub is located within the bilateral anterior temporal lobes (ATL; see Fig. 1).

The ATL hub hypothesis has been principally driven by cognitive neuropsychology and, in particular, the detailed study of patients with a disorder known as semantic dementia (SD). SD patients present with a progressive yet highly selective central impairment of semantic memory. The deficits are evident in both expressive and receptive semantic tasks, across all modalities including spoken and written language, object use, picture-based tasks, environmental sound tasks, and in olfaction and taste (Bozeat et al., 2000; Coccia et al., 2004; Lambon Ralph et al., 2001; Luzzi et al., 2007; Piwnica-Worms et al., 2010). Strikingly, other perceptual and cognitive faculties, such as phonology, executive skills and memory for recent events, remain largely unaffected (Gorno-Tempini et al., 2011; Hodges et al., 1992; Irish et al., 2011).

The SD syndrome falls within the spectrum of frontotemporal dementia (FTD) and is coupled with relatively focal atrophy and hypometabolism centred on the polar and ventrolateral aspects of the bilateral anterior temporal lobes (Mummery et al., 2000; Nestor et al., 2005). The body of evidence for a role of the ATL as a semantic hub is now extensive and includes convergent observations from functional neuroimaging, direct intracranial recording, and also neuromodulation studies of neurotypical adults (Binney et al., 2018, 2016b, 2010; Binney and Lambon Ralph, 2015; Chan et al., 2011; Hoffman et al., 2015; Mion et al., 2010; Pobric et al., 2007; Shimotake et al., 2015). While the CSC framework asserts that the ATL hub is a crucial contributor, it does not assert that conceptualization can be achieved solely by reactivation of the representations served by the hub. Instead, in the model instantiated computationally by Rogers and colleagues (2004), the hub and spokes are bi-directionally connected and complete conceptualization arises from the conjoint computations of both the hub and all the distributed ‘spokes’. Observations from both TMS and fMRI studies support this notion (Guo et al., 2013; Pobric et al., 2010; Reilly et al., 2016).

The second tenet of the CSC framework is that the successful application of conceptual knowledge (i.e., the generation of meaningful behaviour) requires mechanisms that control access to our knowledge. This is necessary because our extensive and varied experiences of words, people and objects result in deep and complex representations, and in many circumstances, we need only to retrieve a few details. Indeed, automatically retrieving all aspects of our knowledge would be computationally expensive and might be inappropriate and/or interfere with our ability to achieve our goals. For example, the pianist need not retrieve all their expert knowledge of how to use their instrument to play a concerto, should, in the very moment, their only task be to move it across the stage (Saffran, 2000).

Control processes are therefore needed to actively shape the way we access our semantic database and ensure that only context- and task-relevant aspects of meaning are brought to the fore. There is evidence to suggest that semantic representation and semantic control can be dissociably affected by brain injury or disease. For example, Jefferies and Lambon Ralph (2006) describe a group of patients with multimodal semantic impairments following stroke who exhibit performance that is inconsistent across semantic tasks and across trials within a task, and performance that can improve considerably with the provision of contextual cues that constrain task requirements. This pattern of impairment is consistent with disordered cognitive control and is associated with damage to ventrolateral frontal and/or posterior perisylvian regions (Jefferies, 2013; Jefferies and Lambon Ralph, 2006). In contrast, SD patients are highly consistent and insensitive to cues. This is congruous with a degradation of semantic knowledge. Observations such as these support the claim that semantic representation and control are associated with distinct cortical territories.

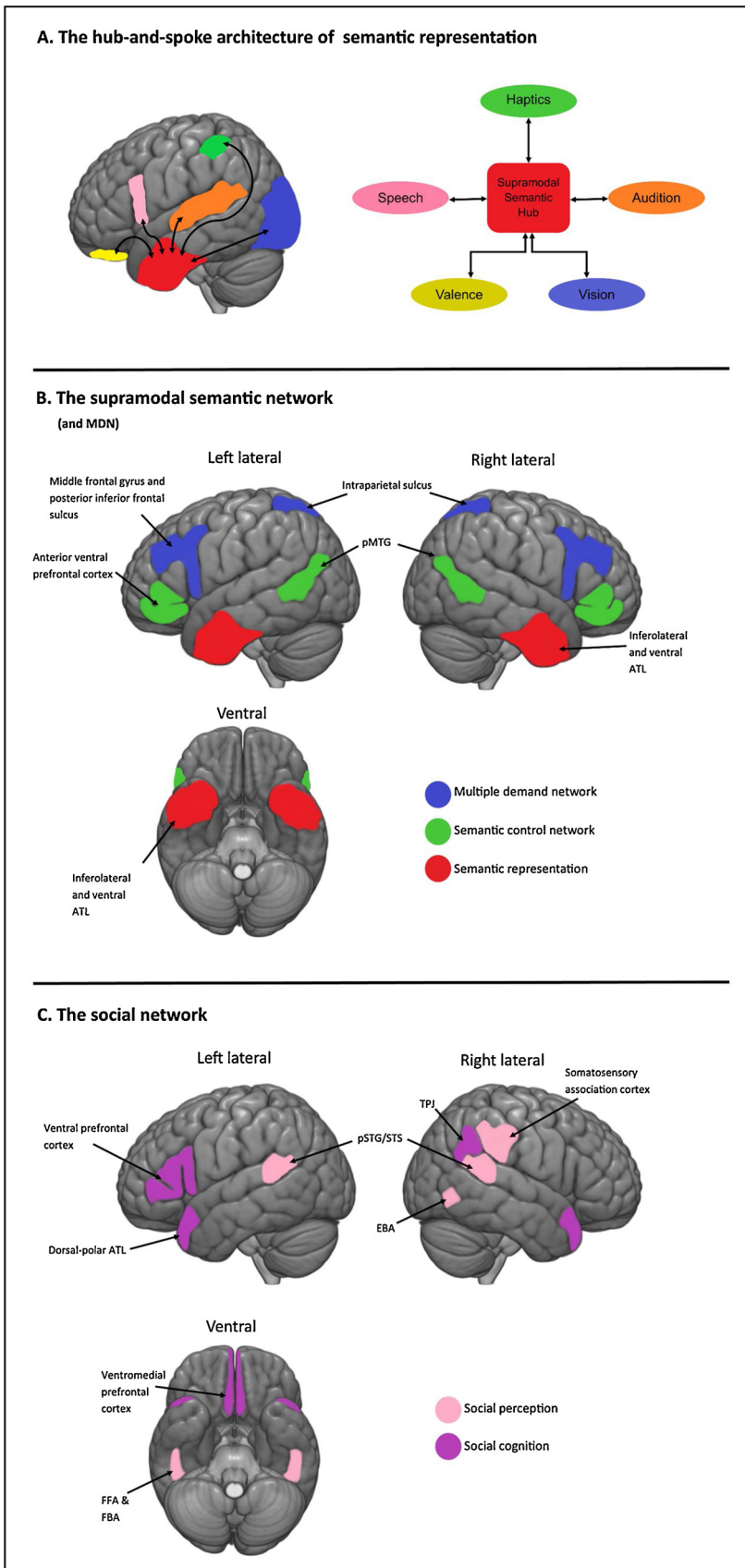


Fig. 1. Brain networks associated with semantic and social cognition. This figure contains simplified schematics of the brain networks purported to be involved in semantic and social cognition. Panel A illustrates the putative hub-and-spoke architecture of semantic representation, and highlights contributions of both modality-specific association cortex, and a supramodal semantic ‘hub’ located in the bilateral anterior temporal lobes. Although not shown here, we acknowledge that medial frontal and parietal association cortex (e.g., the cingulate and pre-cuneus) may also contribute as ‘spoke’ regions. Panel B illustrates the broader supramodal semantic network, which comprises the anterior temporal hub, and frontal and posterior temporal regions implicated in semantic control processes (Lambon Ralph et al., 2016). This is contrasted against regions hypothesised to comprise a domain-general multiple-demand network (MDN; Duncan, 2010). Note that not all regions of the MDN are shown, and some regions overlap with those of the semantic control network (see text for more details). Panel C illustrates lateral and ventral brain regions associated with social perceptual and cognitive processes. This network is also thought to include medial structures such as the dorsomedial prefrontal cortex (Adolphs, 2010). ATL = anterior temporal lobe; pMTG = posterior middle temporal gyrus; pSTG/STS = posterior superior temporal gyrus/superior temporal sulcus; TPJ = temporoparietal junction; EBA = extrastriate body area; FFA = fusiform face area; FBA = fusiform body area.

By now a sizeable body of convergent patient, fMRI, and TMS evidence supports a role for bilateral ventrolateral prefrontal and temporoparietal cortex in shaping or regulating which aspects of meaning are retrieved in both verbal and non-verbal semantic tasks (Badre and Wagner, 2007; Noonan et al., 2009; Thompson-Schill et al., 1997; Thompson et al., 2016; Whitney et al., 2011a). Recent investigations have therefore begun to tease apart the individual contributions of these regions to semantic control and establish the extent to which they are distinct from domain-general executive processes (Davey et al., 2016; Devlin et al., 2003; Gough et al., 2005; Noonan et al., 2013). Indeed, the CSC framework proposes that the executive component of semantic cognition comprises both domain-general processes and processes specific to semantic memory retrieval. Domain-general control processes support goal-driven behaviour and respond to associated executive demands irrespective of the task domain (i.e., perceptual, motor or semantic; Duncan, 2010). Such processes recruit nodes of the Multiple-Demand network including the middle frontal gyrus and posterior inferior frontal sulcus and the intraparietal sulcus (Duncan, 2010). Semantic retrieval demands, however, specifically correlate with activation of more inferior structures, including the ventrolateral prefrontal cortex (particularly pars orbitalis of the inferior frontal gyrus) and the posterior middle temporal gyrus (see Fig. 1B; Badre et al., 2005; Fedorenko et al., 2012; Nagel et al., 2008; Whitney et al., 2011b). CSC proponents have suggested that these additional regions in inferior frontal and posterior middle temporal gyri could play a role in mediating the interaction of domain-general control processes with the semantic representational system (Davey et al., 2016; Lambon Ralph et al., 2016).

Indeed, a final key feature of the CSC framework is that the representational and control systems do not act in isolation (Lambon Ralph et al., 2016). Instead, it has been proposed that the mature semantic system is best characterised by these two principal systems, as well as by their interaction. Initial efforts to test this proposal empirically support this idea. For example, fMRI evidence has begun to elucidate the way in which the semantic control network interacts with the hub-and-spoke architecture underpinning semantic representation; Chiou et al. (2018) observed that the control system dynamically modulates its connectivity with hub and spoke regions according to semantic content and difficulty of tasks.

3. The CSC framework and sociocognitive processing

In this section, we apply the principles and basic architecture of the CSC framework to social information processing. Our premise is that in doing so, we can open up a new understanding of social cognition, revealing that it operates under the same basic principles as semantic cognition and that it implicates a highly overlapping, if not the same, set of brain regions (see Fig. 1).

Adolphs (2010) describes three broad stages of social information processing, namely *perception*, *cognition*, and *regulation*. It is our assertion that these stages map transparently onto the CSC framework. Adolphs (2010) describes social perception as the transduction of social information towards a richer representation required for cognitive level processing. In other words, social perception is the sensory detection of other agents in the environment and signals from this process are used by other cognitive architectures. This is not dissimilar to the description of the role played by modality-specific spokes in the CSC framework as semantic entry/exit points that translate between sensation/motor representations and semantic knowledge (Lambon Ralph, 2014). Social perception includes the *visual* perception of faces and biological motion, the *auditory* perception of speech and paralinguistic cues, the *olfactory* detection of pheromones, and the *somatosensation* of affective touch, to name but a few of the wide array of multimodal inputs that inform our social experiences and form the building blocks of social knowledge.

Broadly speaking, the processing of each of these social perceptual signals can be subsumed under one of the spokes of the CSC framework

(Fig. 1A), and this prompts interesting questions about modality specificity within social information processing. One such question concerns the degree to which brain regions engaged by social perceptual signals overlap with those engaged by perceptual processing more generally and, conversely, whether functional sub-divisions exist within modality-specific processing streams that amount to privileged pathways for socially-relevant perceptual inputs. The degree of overlap is unclear, stemming from the fact that research questions in this domain tend to emphasise divergence of function rather than convergence. Indeed, the topic of domain-specificity in social perception is subject to a rich debate that extends beyond the scope of this paper, but suffice it to say that there are certainly indications that sub-specialisations do exist (for reviews, see Adolphs, 2010; Kanwisher, 2010; Spunt and Adolphs, 2017). The CSC framework, however, is equivocal on this issue, as the structure of the overall model is not tied to the degree of domain or category-selectivity in the spokes. A further question concerns whether some spokes could be particularly important for social cognition, as compared to semantic cognition more generally. Indeed, the CSC framework acknowledges that some sources of modality-specific information (e.g., emotional valence) will be differentially important for some types of concept (e.g., abstract social concepts; Binney et al., 2016b; Crutch et al., 2013; Kousta et al., 2011; Lambon Ralph et al., 2016).

As for social cognition, Adolphs (2010) describes this as attributional and inferential processing that allows us to go beyond the present inputs and generate knowledge about something that we cannot observe directly. According to the CSC framework, abilities of this nature require access to conceptual-level information that is represented within the anterior temporal lobes (Lambon Ralph et al., 2016). Indeed, the ATL has been linked with social-affective behaviour both in humans and non-human primates (Gallate et al., 2011; Klüver and Bucy, 1939; Simmons and Martin, 2009), and across a range of social processes, including the attribution of mental states (Frith and Frith, 2003), morality (Moll et al., 2005) and processing of affect (Wicker et al., 2003). Regarding humans, there is limited evidence from fMRI (owed, at least in part, to technical challenges associated with obtaining BOLD signal from this region; Binney et al., 2016b), but this is bolstered by descriptions of FTD patients that associate ATL atrophy with profound disturbances in social behaviour including blunted affect, decreased empathy and deficits in receptive emotional processing (Chan et al., 2009; Edwards-Lee et al., 1997; Perry et al., 2001). These observations have prompted several research groups to propose that the ATL plays a domain-specific role in the representation of social knowledge, including person knowledge, emotions, and other more abstract social concepts (Olson et al., 2013; Thompson et al., 2003; Zahn et al., 2007).²

Research efforts aimed at delineating the functional properties of the ATL have recently begun to ask if, and how, the purported roles of the ATL in both social and semantic processes can be reconciled under a single unifying framework (Binney et al., 2016b; Rice et al., 2018b). Some clues already existed within classic comparative neurological studies of bilateral, full depth ATL resection in non-human primates (Brown and Schafer, 1888; Klüver and Bucy, 1939) which, in the contemporary literature, are most commonly cited for post-operative changes in social behaviour. The original aims of these studies, however, were to establish whether bilateral ATL lesions led to associative as opposed to apperceptive visual agnosia. Indeed, they did, but Klüver and Bucy (1939) also noted that in addition to having acquired an inability to generate the meaning of visual stimuli, the primates could also no longer understand familiar auditory stimuli. As such, Klüver and Bucy observed a symptom complex comprising multimodal semantic impairments, plus additional social-affective disturbances, that closely mirror those observed in semantic dementia.

² See Leshinskaya et al. (2017) for a discussion regarding a possible role of a non-ATL region in social conceptual representation.

What appears, therefore, to be a pervasive coupling of semantic and social impairment in the context of bilateral ATL damage is highly suggestive of a more general semantic contribution of the ATL. Indeed, a general semantic contribution would predict that the ATL plays a role in activation of all conceptual information, including that which is socially-relevant. However, it is also possible that the bilateral ATLs comprise a domain-general semantic hub, plus other sub-regions with functional specialisations that are relatively more attuned to certain types of knowledge (Gainotti, 2015; Skipper et al., 2011). Indeed, proponents of the CSC framework have recently argued that there are graded differences in the relative specialisation of semantic function across the bilateral ATL (Lambon Ralph et al., 2016; Rice et al., 2015). This is hypothesised to arise from differential connectivity to each of the modality-specific spokes (Binney et al., 2012; Jung et al., 2017; Plaut, 2002).

According to the “graded” hub-and-spoke model, a ventrolateral ATL region (comprising the anterior fusiform and inferior temporal gyri) is hypothesised to be the centre-point of the semantic hub. This region has a supramodal, and domain/category-general semantic function (Abel et al., 2015; Binney et al., 2016b, 2010; Chan et al., 2011; Hoffman et al., 2015; Shimotake et al., 2015). Away from this point, peripheral ATL sub-regions have stronger connectivity to certain modality-specific systems, and their responses to semantic tasks are more nuanced. For example, recent fMRI studies suggest that while the ventrolateral ATL responds equally to all types of concepts, the dorsal-polar ATL is more tuned to social stimuli (Binney et al., 2016b; Rice et al., 2018b). This may follow from this subregion’s close proximity to and strong connectivity with the limbic system (via the uncinate fasciculus; Bajada et al., 2017; Binney et al., 2012; Papinutto et al., 2016), and could reflect a specialisation in the assimilation of emotion-related information into coherent semantic representations (Olson et al., 2007; Rice et al., 2015; Vigliocco et al., 2013).

A related debate concerns the possible lateralisation of ATL involvement in social versus general semantic cognition (Gainotti, 2015). For example, it has been proposed that the right ATL is specialised for social semantic processing (Zahn et al., 2009). There is limited fMRI evidence to support this claim (e.g., Zahn et al., 2007) but more compelling is the observation that socio-affective impairments in semantic dementia are often more pronounced when the typically asymmetric patterns of bilateral ATL atrophy are greater in the right than the left hemisphere (Chan et al., 2009; Edwards-Lee et al., 1997; Perry et al., 2001). However, an elegant longitudinal patient study by Kumfor et al. (2016) revealed that increasing levels of behavioural impairment correlate with the progression of atrophy in both the left and right ATL. Even more problematic for claims of social domain-specificity is a recent meta-analysis of fMRI studies (Rice et al., 2015) and two further original studies (Binney et al., 2016b; Rice et al., 2018b) that reveal a) bilateral ATL involvement in processing non-social stimuli and b) very little evidence of asymmetric ATL activations to social stimuli. This does not preclude, though, the possibility of graded differences in sensitivity to social information across the left and right ATL (Binney et al., 2016a; Pobric et al., 2015; Snowden et al., 2018). A rightwards bias in this regard could conceivably arise from a division of labour in the representation of certain types of conceptual information or from greater proximity and greater connectivity to certain right-lateralised and socially-salient perceptual pathways such as that involved in face perception (Coad et al., 2017; Gainotti, 2015; Hoffman and Lambon Ralph, 2018; Papinutto et al., 2016; Rice et al., 2018a; Von Der Heide et al., 2013).

As far as we aware, to date, no explicit attempts have been made to determine whether regions that respond to semantic control demands (i.e., the anterior IFG and the posterior MTG) are similarly engaged by the types of tasks and stimuli employed within the social neuroscientific literature. Thus, it remains to be seen how well the control component of the CSC framework maps onto social ‘regulation’ (Adolphs, 2010). In the next two sections, we discuss how key research questions that

pertain to social control might follow along similar lines to the principles explored above in the context of social perception and social cognition. That is, we raise the issue of *specificity* of purported function (e.g., is a regional response related to general cognitive function, a general semantic function, or a domain-specific, social semantic function?) and whether such a distinction should be considered *absolute* or *graded* in nature.

4. How does the CSC framework compare to other models of social cognition?

To further contextualise our proposed application of the CSC framework to account for social behaviours, we compare its features with those of other prominent models of social cognition. Moreover, we compare it to two types of existing model. First, we contrast it against broad models of social cognition that outline general principles that should apply across a range of sociocognitive processes (e.g., Adolphs, 2009; Frith and Frith, 2011; Lieberman, 2006). This enables a cross-examination of high-level assumptions regarding key organisational principles of social cognition, and brain function more generally. Second, we compare tenets of our model to those that have emerged from within a specific domain of social cognition, namely the phenomenon of ‘automatic imitation’ (Brass et al., 2009; Brass and Heyes, 2005; Darda et al., 2018; de Guzman et al., 2016; Gowen and Poliakoff, 2012; Heyes, 2011; Ramsey, 2018; Sowden and Shah, 2014; Spengler et al., 2009; Wang and de Hamilton, 2012). We have chosen to focus on automatic imitation partly for convenience, in that we have experience in this area of research, but also because it provides a specific concrete example of how the general principals of the model can be applied within a specific research context.

Before going further, it is important to highlight one general distinction between the model put forward here and prior models of social cognition, which is that we start from a position of proposing that social cognition is a case of semantic cognition. We are therefore arguing against claims that social cognition is a special or distinct case of cognition. Instead, we suggest that social information processing is just one way of gathering meaning from the environment. The implication here is that social cognition will rely on the same basic cognitive and brain mechanisms as semantic cognition, which includes a sub-system of conceptual representation (the hub and the spokes) and another of control. Existing models of social cognition, whether pitched at a general level or more specifically tied to a particular aspect of social processing (e.g., imitation), have different starting points. Indeed, the key driving force for most has been to characterise mechanisms that are specialised towards social information processing. We argue that this new conceptualisation, which places greater emphasis on more general mechanisms, holds potential to shine new light on the possible structure of the cognitive and neurobiological mechanisms that underpin social information processing.

4.1. A comparison of the CSC framework to general models of social cognition

As outlined in Sections 2 and 3, the CSC framework makes a clear distinction between *representation* and *control*, both in terms of cognitive processes and associated neural networks. Most general models of social cognition place little, if any, emphasis on this differentiation (Adolphs, 2009; Frith and Frith, 2011, 2010; Lieberman, 2006). Further, prior models have only briefly touched upon the contribution of executive processes to social behaviour. For example, Frith and Frith (2011) briefly refer to a “supervisory system” (Beck and Kastner, 2009), which has the hallmarks of executive control, but is otherwise under-specified. Likewise, Adolphs (2009) refers to cognitive control and the engagement of lateral prefrontal cortex, but again, it receives a secondary focus. Moreover, the anatomical specificity of such a supervisory system is lacking. The result is a nebulous construct of social

regulation, and a lack of indication as to whether it is underpinned by systems that are specialised to support social information processing, by more domain-general mechanisms, or by a combination of both types of mechanism.

This state of understanding the systems underpinning social control stands in stark contrast to discussions surrounding social perception and social cognition where great care has been taken to a) define what is socially-relevant information (e.g. pheromones) and what is not, and b) test the extent to which processing this information relies on a specialised set of neural circuits (e.g., person perception in the ventral visual stream, the ‘mirror neuron’ system, and the putative ‘theory of mind’ network; e.g., Adolphs, 2010; Kanwisher, 2010). For a field that has emerged over the past 25 years, this makes sense as a place to start, in terms of establishing the face validity of social cognition as a unique entity to other general forms of cognition. However, by neglecting to also consider the contributions of more domain-general systems to both the representation of social knowledge, and to the regulation of the way we implement this knowledge, these broad models of social cognition may have unintentionally limited their explanatory power. Indeed, we propose that a more comprehensive model of social cognition can only be realised with the concurrent consideration of contributions from both domain-general and domain-specific resources. Moreover, we propose that it is essential to delineate and understand the contributions of both representational and control systems, and the interactions between them.

Rather than frame a putative distinction as one of representation and control, prior models of social cognition have often juxtaposed *controlled* processes against *automatic* processes (Adolphs, 2009; Frith and Frith, 2011; Lieberman, 2006). Typically, automatic processes are characterised as fast, efficient and unintentional, and are contrasted against controlled processes which are slower, less efficient and more deliberate (Posner and Snyder, 1975; Shiffrin and Schneider, 1977). These “dual-systems” approaches have been influential in developing the modern understanding of cognition, but, equally, they have been criticised for oversimplifying both the distinction and relationship between automaticity and control (Bargh, 1994, 1989; Melnikoff and Bargh, 2018; Moors and De Houwer, 2006).

In contrast, we propose that the degree to which behaviours have particular attributes (e.g., speed, efficiency, or intentionality), does not simply reflect the preponderance of one mechanism over the other but, instead, a qualitative difference in the degree to which control needs to be imposed on activation within the representational system. For instance, when looking for a friend at a crowded train station, cognitive control resources would upregulate the importance of face and body feature detection processes that predominantly occur in the ‘spokes’. However, when waiting for a train at a crowded station, attentional resources would prioritise the detection of moving objects rather than faces and body parts, thus leaving face and body-selective modules to operate in a more stimulus-driven and automatic way. As an alternative example, when faced with the task of evaluating the commonalities between two familiar persons, our conclusions would be quite different when we base the comparison on, subjectively speaking, the most salient and thus automatically-retrieved features (e.g., their professional relationship to us) versus more latent features (e.g., their personal values and hobbies). Therefore, depending on the social context, there is a need to exert quantitatively stronger control influences to inhibit the retrieval of certain aspects of representational content. In addition, there might also be a need for qualitatively different kinds of control, such as control exerted through domain-general resources in some contexts, but semantic control resources in other contexts (Ramsey, 2018). In all contexts, however, we suggest that the processing of social information would require some degree of representational input and some form of cognitive control. Therefore, following precedent in the domain of theory-of-mind (Carruthers, 2017, 2016), we are proposing a single route architecture that has as much explanatory power as the dual-route approaches previously outlined.

Our proposal has some overlap with those put forward by others recently (Amodio, 2019; Kilner, 2011; Spunt and Adolphs, 2017), all of which emphasise the consideration of parallel literatures for understanding mechanisms of social information processing. For example, partly based on principles developed in models of memory (Cabeza and Moscovitch, 2013), Spunt and Adolphs (2017) argue that social cognition may be made up of multiple component pieces, and not all of them need to be domain-specific. Moreover, Amodio (2019) argues that models of impression formation can be constrained by the way types of memory rely on functionally and anatomically distinct systems. Of particular note for our proposal, is Kilner’s (2011) suggestion that understanding of the meaning of observed actions is mediated by a semantic retrieval pathway between anterior IFG and posterior MTG. Indeed, this is consistent with our suggestion that social regulation, or social control, is underpinned by the very same brain systems that support semantic control more generally. An implication of these combined perspectives is that existing models within parallel domains of cognition may provide more fertile ground for building models of social cognition than is currently afforded by building them as a distinct or even special case.

To be clear, though, we are not suggesting that processing social information does not impose exceptional demands on cognition. To the contrary, we acknowledge that many social signals are amongst the most complex stimuli to interpret. What we are instead suggesting is that processing social information may differentially engage certain parts of the semantic system, such that graded differences will emerge in the responses of the associated neural network to more or less socially-relevant tasks. As we discussed in the previous section, evidence already exists to support this notion, and in particular that of a graded representational semantic hub in the bilateral ATLs that comprises pan-category general semantic function in the ventrolateral area and more nuanced social semantic function within the temporopolar cortex (Binney et al., 2016b; Rice et al., 2018b)

4.2. A comparison of the CSC framework to models of automatic imitation

Our model emphasises a more generalizable set of multiple demand and semantic control processes (Fig. 2A), rather than any form of social domain-specific control as proposed in models of automatic imitation and processes associated with regulating self-other processes (Brass et al., 2009; Sowden and Shah, 2014; Spengler et al., 2009; Wang and de Hamilton, 2012). Indeed, as briefly discussed above, the starting point of the current model is that we should expect the control of social representations to be identical in structure to the control of non-social representations. For example, sitting down on a chair will involve visual and motoric representations, plus a sense of timing, all constrained by a relatively stable context (e.g., the chair’s condition). These visual and motoric representations would need to be appropriately controlled to successfully carry out the action. Likewise, interacting with a person, in terms of cognitive systems, may be no different. We have a set of person representations – visual, motoric, affective – which need controlling in reference to an interpersonal context that may be constantly-shifting (e.g., a colleague’s evolving perspective of an argument you are delivering).

When considering the evidence for or against this model, it is important to be mindful of the difference between stimulus-specificity and mechanism-specificity (Adolphs, 2009). For example, there is a large body of evidence to support the existence of brain regions that are relatively specialised for the social information represented by faces, bodies, voices and for reasoning about others’ mental states (Kanwisher, 2010). These regions appear distinct from those associated with processing objects (Bar, 2004), tools (Culham and Valyear, 2006), places (Epstein et al., 1999) and written words (Dehaene and Cohen, 2011). This suggests a degree of stimulus specificity in detecting aspects of the social vs. non-social environment. However, less evidence exists for mechanism-specificity in terms of controlling the activation associated

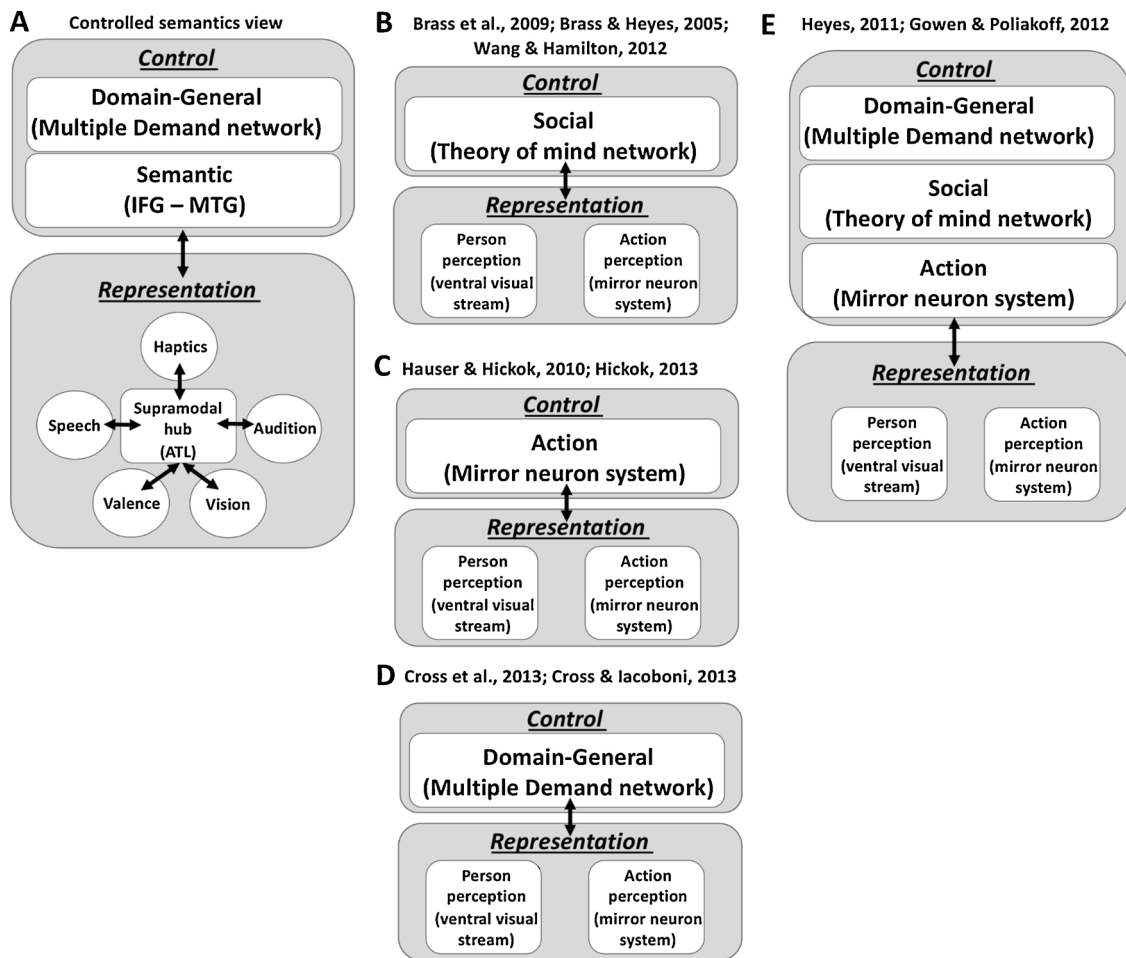


Fig. 2. Models of social information processing in the control of automatic imitation.

with such social representational content. On the contrary, considerable evidence exists to support the involvement of more domain-general control systems that span frontoparietal cortices (Badre, 2008; Corbetta et al., 2008; Corbetta and Shulman, 2002; Desimone and Duncan, 1995; Duncan, 2010; Miller, 2000).

In the context of research concerning automatic imitation, several forms of domain-specific control or “social control” have been proposed (Fig. 2B). For example, Brass and colleagues (2009) suggest that a brain circuit believed to be involved in mental state attribution is engaged when imitative tendencies need controlling during social interactions (see also Brass and Heyes, 2005; Spengler et al., 2009; Wang and de Hamilton, 2012). More specifically, Brass and colleagues (2009) suggest that anterior medial prefrontal cortex (mPFC) and right temporoparietal junction (rTPJ), two key nodes of the putative theory of mind network (Frith and Frith, 1999; Saxe and Kanwisher, 2003; Van Overwalle, 2009), regulate social interactions through a process of self-other distinction. In other words, it is claimed that by separating self from other during social exchanges, mPFC and rTPJ play an important role in the regulation of social interactions.

Based on the initial work by Brass and colleagues (Brass et al., 2009; Brass and Heyes, 2005; Spengler et al., 2009), which provided the first account of “social control” in automatic imitation, several variants based on this theme have followed. For instance, Wang and de Hamilton (2012) have suggested that social control is governed through the theory of mind network exerting a top-down influence on other neural networks associated with social cognition. By contrast, other researchers have proposed that a process of self-other distinction, which is underpinned by rTPJ, is engaged in a more elaborate set of social cognitive functions, which extend beyond imitation, and include

perspective-taking, empathy and theory of mind (de Guzman et al., 2016; Sowden and Shah, 2014). Moreover, disruption to this process has been proffered as an important contributing factor to social disorders such as autism spectrum conditions (de Guzman et al., 2016). An alternative domain-specific proposal suggests that the control of imitation relies on the operations of the mirror neuron system (Fig. 2C; Hickok, 2013; Hickok and Hauser, 2010). The mirror neuron system is activated during the performance and observation of action and has previously been suggested to be involved in imitation (Iacoboni, 2008). These accounts all suggest that there exists a specialised control circuit for regulating interactions with other people.

Some other proposals leave open the possibility of a contribution of domain-general control in imitation (Fig. 3D; Cross et al., 2013) or a combination of both forms of control – domain-general and domain-specific (Fig. 3E; Cross et al., 2013; Gowen and Poliakoff, 2012; Heyes, 2011). For example, Gowen and Poliakoff’s (2012) model includes a role for mPFC in regulating similarity to self, a process specific to social cognition, whereas lateral prefrontal cortices are involved in more domain-general processes including the regulation of attention and inhibitory control. The implication here, and one that we advocate, is that should specialised control mechanisms exist, they will be nested among and complement more general executive processes.

One of the key arguments of our proposal is that the field needs to prioritise investigating how far models of social cognition get when they use broad and encompassing definitions of executive and representational systems that have been established across other domains. It is our view that before claims can be made about the existence of, or need for, social domain-specific control processes, future empirical work must first firmly establish that domain-general and

semantic control processes are insufficient to account for the social psychological phenomenon at hand. To this end, experimental designs should always attempt to dissociate the social aspect of an experiment from the other key manipulations (e.g., executive load) and, for example, establish an interaction wherein the effect of interest (be it behavioural or physiological) is only present when the task or stimuli are socially-relevant. Furthermore, we believe that it is essential that the generality of an effect is comprehensively explored by testing over a wide range of experimental paradigms and using a variety of measures (behavioural and brain-based) and populations (neurotypical and clinical). This serves to avoid unnecessary fractionation and an explosion of putative control processes, which serve all manner of conceivable sub-domains – e.g., imitation, emotion, trait inference, etc. By integrating more domain-general and semantic control mechanisms into our model of social cognition, rather than minimising their role or ignoring them completely, we aim to harness the benefits from prior literature that characterises the contribution of a highly developed and powerful set of executive functions (Corbetta et al., 2008; Duncan, 2010; Lambon Ralph et al., 2016). We are not suggesting that social cognition would be any less sophisticated or interesting if it were not to rely exclusively on domain-specific processes (Spunt and Adolphs, 2017).

By looking at a particular test case – the study of automatic imitation – it is easy to see how the pursuit of domain-specific processes may have overshadowed a role of more generalisable systems. Although researchers may be ultimately aiming for the same end, which is to understand cognitive and brain mechanisms that underpin specific social behaviours, there may have been misalignment between attempts to understand stimulus specificity and mechanism specificity. By emphasising the potential contribution of domain-general processes, we provide a reminder to clearly distinguish between the type of information in the environment (social or otherwise) and the type of mechanism that processes such information (i.e., the level of selectivity).

5. How can the CSC framework guide future social cognition research?

We offer four recommendations for future social cognition research guided by the CSC framework. First, and quite simply, we propose that when alternative models are being formulated, it would be useful to at least consider the concepts of representation and control, and the degree to which they are dissociable. Indeed, providing clear definitions of a model's architecture (including the associated neuroanatomy) and component processes enhances the ability to compare and contrast one theory to another (Gray, 2017). Many of the social cognition theories covered in this paper do not make explicit reference to terms such as these, and we suggest they may benefit from doing so. It could, for example, be particularly important for understanding commonalities and differences in the functions ascribed to certain brain regions. As outlined in Fig. 2, diagrammatic illustration of model spaces can help researchers communicate in a common language. To be clear, though, we are not proposing that the CSC framework and the associated terms are the only way to characterise social cognition. Rather, much like in many other domains of research, we are suggesting that investigators from the social cognitive neurosciences could take steps towards developing formalised approaches that aid effective and informative comparison of models and ideas (Lenartowicz et al., 2010; Poldrack et al., 2011).

Second, we argue against an *a priori* need for domain-specific social processes. Rather, we suggest greater consideration needs to be given to a role of more generalizable systems and processes which operate in social contexts because they operate in every context (to some extent). Only when more general mechanisms cannot explain findings, may it be sensible to consider domain-specific “social” processes. For example, future research into executive processes in social cognition should

explicitly model, and empirically examine, the role of domain-general control alongside any proposed form of domain-specific “social control” (see Section 4.2 for practical examples; Brass et al., 2009; Brass and Heyes, 2005; de Guzman et al., 2016; Sowden and Shah, 2014; Spengler et al., 2009; Wang and de Hamilton, 2012). This also includes acknowledging the possibility that domain-general control processes interact with domain-specific social representations (Darda et al., 2018; Ramsey, 2018). Such a position statement reinforces the important distinction between the ‘socialness’ of information in our environment and that of mental processes. That is, social information and processes (e.g., faces, displays of emotion, social judgments etc.) are no less social if they are partly underpinned by mental processes that operate in many domains (i.e., both social and non-social contexts). Although this distinction appears to be an obvious point to make, and indeed, it has been made before (Adolphs, 2009), its significance for theory development in social cognitive neuroscience is frequently underappreciated.

A third influence on future research is the potential for the CSC framework to inform cognitive models that account for atypical or disordered social cognition, including autism spectrum conditions and schizophrenia as well as acquired social dysfunction observed following stroke, and in neurodegenerative disease. The simple distinction between representation and control has been proven to be clinically-relevant in the case of central semantic disorders. Patients with quantitatively similar panmodal semantic impairments have been shown to dissociate on the basis of qualitative error patterns that are consistent with either degraded/lost representations or dysregulated access to representations. Disorders of representation are associated with bilateral ATL pathology, while semantic control impairments arise following frontal and/or temporo-parietal damage (Jefferies and Lambon Ralph, 2006; Thompson et al., 2016). It might also be interesting to consider whether future research might similarly dissociate social disorders on the basis of representation versus control impairments. Some insight comes from neuropsychological investigation of frontotemporal dementia (FTD) where apparently similar clinical presentations of social dysfunction arise in the context of different patterns of brain atrophy and different aetiologies (Binney et al., 2016a; Kamminga et al., 2015). It is now becoming apparent that in FTD variants with more prominent frontal lobe damage, the social impairments can be linked to deficits in executive function, while patients with greater temporal lobe than frontal lobe damage demonstrate a much weaker association (Healey and Grossman, 2018; Kamminga et al., 2015). In addition, in each of these disorders or diseases, it may be the *interaction* between representation and control that operates in an atypical manner. As a consequence, when tested in isolation, systems for representation and control could operate in a perfectly “normal” manner, whilst these individuals would still have atypical profile of cognitive function overall.

Finally, the current paper was focussed upon models of mature neurocognitive systems. We did not consider, in any detail, the emergence of social cognitive processes (Weigelt et al., 2014). However, we recognise potential for our proposal to aid in the advancement of neurocognitive models of social development. In particular, we argue that because social cognition is a case of semantic cognition then, over the course of development, the former should emerge from the latter. Such a proposal is consistent with the Neuroconstructivist and Neuroemergentist perspectives (D'Souza and Karmiloff-Smith, 2016; Hernandez et al., 2019; Karmiloff-Smith, 2015, 2006), which posit that the development of complex cognition, including social cognition, involves the combination of relatively simpler antecedent cognitive building blocks. A testable prediction that arises from this is that semantic and social cognition might be less easily distinguishable at earlier than later stages of development, and this may manifest in either behavioural patterns or in the engagement of brain networks.

6. Concluding remarks

A major challenge for the cognitive sciences is to characterise how we understand others and coordinate our behaviour to achieve mutually beneficial outcomes (Frith and Frith, 2010). In the above, we have outlined a novel theoretical framework for understanding social behaviour. Counter to a recent trend in delineating highly domain-specific models, this approach delivers clear foundational principles that can be generalised to a number of social phenomena, and can be translated into straightforward and testable predictions. Moreover, with time, it may emerge as having great potential to influence understanding of social impairments and the development of associated interventions. Alongside this framework, we provide suggestions of how to develop formalised approaches that could aid effective and informative comparison of models and ideas in the domain of social neuroscience, and cognitive science more generally. In sum, by treating social cognition as just one of the many ways in which we gather meaning from the world, rather than a special case, there is potential to shine new light on the cognitive and neurobiological mechanisms that underpin social information processing, and radically advance our understanding of human interactions, both in health and in disease.

Declaration of Competing Interest

The authors declare no potential conflicts of interest.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.neubiorev.2020.01.030>.

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