



## Supplementary motor area as key structure for domain-general sequence processing: A unified account



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### ABSTRACT

The Supplementary Motor Area (SMA) is considered as an anatomically and functionally heterogeneous region and is implicated in several functions. We propose that SMA plays a crucial role in domain-general sequence processes, contributing to the integration of sequential elements into higher-order representations regardless of the nature of such elements (e.g., motor, temporal, spatial, numerical, linguistic, etc.).

This review emphasizes the domain-general involvement of the SMA, as this region has been found to support sequence operations in a variety of cognitive domains that, albeit different, share an inherent sequence processing. These include action, time and spatial processing, numerical cognition, music and language processing, and working memory.

In this light, we reviewed and synthesized recent neuroimaging, stimulation and electrophysiological studies in order to compare and reconcile the distinct sources of data by proposing a unifying account for the role of the SMA. We also discussed the differential contribution of the pre-SMA and SMA-proper in sequence operations, and possible neural mechanisms by which such operations are executed.

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## 1. SMA involvement in domain-general sequence processing

The Supplementary Motor Area (SMA) lies in the superior frontal gyrus and is, in humans, located on the medial part of the brain that constitutes the Brodmann's area 6. The SMA comprises at least two subareas that have been considered as anatomically and functionally distinct: the pre-SMA (rostral part) and the SMA-proper (caudal part) (Lehéricy et al., 2004; Matsuzaka et al., 1992; Picard and Strick, 2001). Pre-SMA is connected to the prefrontal cortex (Bates and Goldman-Rakic, 1993), whereas SMA-proper projects directly to the primary motor cortex (M1), dorsal premotor cortex (PMd) and the spinal cord (Bates and Goldman-Rakic, 1993; Luppino et al., 1993; Tanji, 1996). Both subareas are connected to the basal ganglia (Postuma and Dagher, 2006; Draganski et al., 2008).

SMA is traditionally considered a key region for motor planning and execution, and is thought to be involved in self-initiated movements (Passingham et al., 2009), action monitoring (Bonini et al., 2014), response inhibition (Mostofsky and Simmonds, 2008; Nachev et al., 2008) and action sequencing (Tanji, 2001). In particular, the pre-SMA would be preferentially involved in higher-level planning processes while the SMA-proper would be more strictly associated with motor execution (Picard and Strick, 2001; Nachev et al., 2008; Tanji 1996).

A recent review highlighted the involvement of SMA in non-motor functions, suggesting that SMA is not simply a motor structure but also subserves more “cognitive” processes (Nachev et al., 2008; see also Leek and Johnston, 2009). In fact, SMA appears to be involved in a broad range of cognitive domains, being implicated in timing (Casini and Vidal, 2011; Coull et al., 2016; for reviews), spatial processing (Bahlmann et al., 2009; Leek et al., 2016), numerical cognition (Arsalidou and Taylor, 2011), working memory (Rottschy et al., 2012), language (Segaert et al., 2012), music perception and production (Bengtsson et al., 2009; Donnay et al., 2014).

These cognitive domains are very different from each other: composing a melody is completely different from solving an arithmetic operation, just as perceiving the passage of time is completely different from orienting the attention to space. In light of this, we put the same question presented in the review by Nachev et al. (2008) again: what does the SMA do?

In order to understand the role played by the SMA, it appears to be useful adopting the “Ockham razor” or, in other words, the law of parsimony. Based on this, it seems unlikely that SMA is involved in operations that are specific to each of the domains mentioned above (i.e., *domain-specific hypothesis*). Rather, a more parsimonious explanation is that SMA plays the same role among these distinct domains (i.e., *domain-general hypothesis*), subserving cognitive operations that are shared by all of them. This view is also driven by recent studies, which proposed hybrid models for the neural representation of cognitive processing in the human brain, based on both modular and holistic principles (Fehr, 2013; Fuster, 2009, 2006). Networks in the human brain are indeed hierarchically organized. At the bottom of this organization, neural networks are small and represent relatively simple percepts or motor acts (i.e., *domain-specific representations*), whereas at the top of the organization, neural networks are wider, involve hetero-modal association cortices, represent ‘more complex’ and abstract information, and thus have a domain-general role (Fehr, 2013; Fuster, 2006). In particular, the frontal regions are organized in an executive hierarchy departing from primary motor cortex, through intermediate premotor and SMA areas and toward prefrontal areas, which encode the most general and abstract representations (Fuster, 2006).

Assuming a domain-general role of SMA, the next step consists in identifying what operations are common among timing,

spatial processing, numerical cognition, working memory and the other domains mentioned above. Interestingly, all of these seem to entail an inherent sequence processing. Indeed, in order to accomplish these functions, it is necessary to accumulate and integrate sequential elements into higher-order representations. Sequential operations are necessary to create a representation of time (Coull et al., 2015), space (Leek et al., 2016), and other magnitude dimensions, such as numbers (Dehaene et al., 1996). Sequential computations are important in language, for concatenating letters to words, words to phrases, and phrases to sentences (Bahlmann et al., 2009; Segaert et al., 2012), in working memory, for maintaining and updating information given serially (Tanaka et al., 2005), and in music, for integrating sound sequences over time (Leaver et al., 2009). More specifically, all these domains involve the processing of sequences, which can be conceptualized as structures of elements integrated on the basis of particular ordinal and temporal properties (Janata and Grafton, 2003; Ullén and Bengtsson, 2003). Ordinal properties refer to the serial order of the elements in a sequence, whereas temporal properties refer to the serial order of the temporal intervals between such elements. On these grounds, we propose that SMA is involved in domain-general sequence processes, contributing as a hub to the integration of the elements into a sequence, likely by encoding the temporal and ordinal properties of this sequence (Bengtsson et al., 2004; Janata and Grafton, 2003; Schubotz and von Cramon, 2001; Schwartz et al., 2012). Importantly, we emphasize the domain-general involvement of SMA since this region has been found to support the organization of elements into sequence representations, regardless of the nature of such elements (e.g., motor, temporal, spatial, linguistic, numeric etc.).

In this review we describe the most relevant results from neuroimaging, stimulation, lesion and electrophysiological studies that, although exploring very different cognitive functions, have demonstrated a crucial role for SMA in sequence processing, thus suggesting its domain-general involvement (Table 1). We also investigated in more depth which sub-region, between pre-SMA and SMA-proper, is engaged preferentially by sequence processing.

## 2. Cognitive domains where the SMA mediates sequence processing

### 2.1. Action sequences

One of the first domains where SMA was found to be crucially involved is in sequencing of actions (Tanji and Shima, 1994; Tanji, 2001; see Nachev et al., 2008, for a review). Recordings from monkeys have demonstrated that SMA and pre-SMA neurons respond preferentially to a specific order of movements (e.g., turn–pull–push a lever) rather than another (e.g., turn–push–pull) (Tanji and Shima, 1994; Shima, and Tanji, 2000). SMA neurons encode also the relational order of a movement in a given sequence; for example, some of them are active only before the third movement has to be accomplished, regardless of the nature of that movement (Clower and Alexander, 1998; Shima and Tanji, 2000). Moreover, when a GABA (g-aminobutyric acid) agonist was injected into the SMA regions, monkeys were shown to be greatly impaired to perform action sequences even if they were able to execute correctly simple movements (either self-initiated or externally cued). This represents the first evidence that disrupting the SMA activity interferes selectively with sequences of movements, leaving the execution of simpler, single movements unaffected (Shima and Tanji, 1998). As can be seen in Fig. 1, neurons in the pre-SMA in particular seem to monitor movement sequences in a binary manner, with some neurons responding to odd-numbered elements within a behavioural sequence and others responding to

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