Opinion

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The medial prefrontal cortex mediates social event knowledge

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Accumulating evidence from social neuroscience demonstrates that the medial prefrontal cortex (mPFC) is a crucial component of the neural systems mediating social event knowledge. Here, we present an integrative theory of the cognitive and neural bases of social event knowledge. The structural and temporal representation binding (STRing) theory assumes that the mPFC represents abstract dynamic summary representations in the form of event simulators (elators). Elators give rise to social event knowledge via binding with regions in the posterior cerebral cortex and limbic structures. We propose a segregation of elator functions along the dorso-ventral mPFC axis and review neuroscience evidence to support the specificity of elators as the underlying structures for the development of event, person and self schemata.

Structural and temporal representation binding (STRing) theory

Social event knowledge is abstraction derived from concrete experience of social life – its contents originate in human interaction and construct the understanding of the social world. The social brain hypothesis links evolutionary pressure for brain enlargement and specialization to the need of solving problems in socially complex environments [1]. The sophisticated neural architecture of the human prefrontal cortex (PFC), along with the sustained firing of its neurons [2] and the ability to integrate a larger amount of excitatory inputs from many sources [3], provided a vehicle for the emergence of social cognition [4]. In particular, the medial PFC (mPFC) – consisting of medial orbital frontal cortex (mOFC), ventral mPFC (vmPFC) and dorsal mPFC (dmPFC) – has considerably increased in size in recent evolution in the brains of primates and is especially well developed in humans [5]. Because the mPFC is phylogenetically and ontogenetically older than the lateral PFC, a functional dissociation evolved in which the mPFC became capable of encoding stable representation of predictive event sequences compared to adaptive representations of frequently modified event sequences encoded in the lateral PFC [6–11] (Box 1). Over the course of evolution, specialized neural systems in the mPFC emerged that enabled the encoding of social event knowledge into sequentially linked but individually recognizable representations that can be used to guide social goal-directed behavior over a longer period of time [12–15].

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Most current views of PFC function focus on lateral PFC subregions [16–23], whereas a systematic analysis of mPFC subregions in the context of social functions only began recently [24,25]. Non-human primate research has not been particularly helpful in identifying higher-order social mPFC functions. By contrast, accumulating evidence from functional neuroimaging studies in humans has demonstrated that besides the temporal pole, superior temporal sulcus, temporoparietal junction and amygdala [26], the ventral and dorsal parts of the mPFC are also core regions of social cognition [24,25]. Although it is acknowledged that the mPFC mediates social event knowledge [27–30], the underlying neural structures of social event knowledge and the nature of its functional subdivisions within mPFC are still obscure.

Here, we present an integrative 'structural and *t*emporal *r*epresentation bind*ing*' (STRing) theory of the cognitive and neural bases of social event knowledge. The STRing theory relies on the concept of abstract dynamic summary representations [31,32] (Box 2), which has its roots in mechanisms that are grounded both in brain architecture and in principles of neural processing [33]. According to this view, representations have no existence separate from processes, but are instead embedded in, distributed across and hence inseparable from one another [34]. The STRing theory seeks to establish the format and domain specificity of representations according to which the same fundamental processes operate on different categories of information. In particular, we argue that the mPFC represents 'event simu*lators*' (elators) that give rise to social event knowledge via structural and temporal binding with regions in the posterior cerebral cortex and limbic structures. Elators are grounded in the brain's systems and represent the underlying properties for social cognitive structures that are of vital importance for the development of event schemata, person schemata and self schemata.

Social event knowledge and elators

Within the STRing theory, elators are defined as abstract dynamic structured summary representations that are learned and developed over time through direct and indirect perception and experience with social situations (Figure 1). They capture the sequence of previously encountered events that are semantically structured by distinctive features such as agents, actions, objects, mental states and settings. Most widely, elators are temporally organized on the basis of (i) 'goals' that enable the selection

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Box 1. Medial PFC as a time-integrator for social event knowledge

Studies of functional specialization within the PFC have emphasized the distinction between lateral and medial PFC areas [8,9,66]. The lateral PFC encodes adaptive representations of frequently modified event sequences, whereas the mPFC encodes stable representation of predictive event sequences [6,27,29]. The achievement of a stable representation provided humans with an instrument for interpreting and acting on a reality that would otherwise be unpredictable. The social brain is an organ of adaptation that builds its structure through interactions with others. Over the course of evolution, precursors of social event knowledge began to serve specific goals to improve social interaction and intelligence by providing interpretive context for agents, actions, objects, mental states and settings to be found in the social world. As a consequence, specialized neural systems in the mPFC emerged that enabled the encoding of social event knowledge that is intimately involved in both planning and monitoring one's own behavior in addition to understanding and predicting the behavior of others. The capacity to anticipate other people's intentions and behaviors is one key aspect that sets humans apart from others primates [67]. Although primates can accurately predict the goals of their conspecifics, only humans can maintain a separate mental perspective of their own actions and differentiate this from the perspective of others [68]. Particularly, when we explain an individual's behavior in terms of goals, desires or traits, we realize that those mental representations do not necessarily have to agree with our own interpretations or reality of the world.

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of goal-directed event sequences and (ii) 'outcomes' that enable the selection of the affective responses and reward values associated with event goal achievement. Elators are encoded and retrieved on the basis of simulation mechanisms [31,35]. When a social situation is perceived or experienced, feature detectors in relevant modalities of the brain capture modality-specific states, and neurons in nearby association areas store the patterns' features to represent aspects of experience. For example, social perceptual features (e.g. face, voice and body posture of the agent) are captured in the anterior and posterior temporal cortex, action features (e.g. socially centered action sequences) in the pre-motor cortex, and emotional features (e.g. happiness) in limbic structures. Association areas exist at

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Box 2. Abstractions as dynamic summary representations

Abstraction is a central construct in cognitive science, which can be defined as a summary representation of a category of knowledge in long-term memory [69]. There exist three central properties of an abstraction. First, abstractions are closely linked to 'interpretation'. Once a concept for objects and events has been abstracted from experience, its summary representation supports the subsequent interpretation for later experiences. Second, abstractions are organized into 'structured representations'. Abstractions are assembled[0]into structured representations that interpret complex structures, rather than interpreting isolated components of experiences in the world[0]. Finally, abstractions are 'dynamic' summary representations. Instead of a single abstraction representing a category, an infinite number of diverse abstractions can be constructed online to represent a category temporally. 'Simulators' and 'simulations' are key components to abstractions that evolve through mechanisms of modality-specific reenactment. Simulators develop for various types such as objects, events and mental states. Once a simulator exists, it can reenact small subsets of its content as specific simulations. Those simulations serve a wide variety of cognitive functions such as drawing inferences about physical instances in the environment and mental instance in social interaction with other individuals.

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multiple hierarchical levels ranging from posterior association areas to increasingly complex association areas in anterior brain regions [22]. Importantly, the mPFC located at the apex of this hierarchy serves as a convergence zone [36], binding simpler features from different modalities. Specifically, its neurons conjoin patterns of these features across association areas and time, uniquely capturing the semantically structured and temporally organized components of social event knowledge on the basis of goals and event outcomes represented by the social situation.

As multiple instances of the same social situation are perceived or experienced, they recruit similar neural states in modality-specific feature maps and activate similar association areas. As the consequence, neurons in the mPFC capture diverse exemplars of social situations, establishing an elator that encompasses a multi-modal representation distributed throughout the brain's association and modality-specific areas. Recognizing or thinking of a similar situation, a subset of neurons in the mPFC can partially reactivate elator components in the absence of bottom-up sensory stimulation, and inferences about the situation can be drawn via pattern completion with all components simulated [37]. Reenactment of elator content arises through structural and temporal binding by oscillatory firing patterns of neurons with frequencies in the gamma-range [38] of distributed representations stored in spatially separate cortical areas in the posterior cortex and limbic structures [39–41].

Elator functions

Once elators have been abstracted from experience, their dynamic structured summary representations support the interpretation of later social experiences. Components of an elator can be reenacted temporally as 'event simu*lations*' (elations) and tailored to the constraints of the current social situation serving a wide variety of social cognitive functions. In particular, the STRing theory predicts that elators are of vital importance for the development of event schemata, person schemata and self schemata. Those schemata are both overlapping and distinct concepts in social psychology [42,43] and allow the integration of information over time into a more general and abstract notion of social conduct such as categorizing social entities and events, drawing social inferences and planning and remembering social interactions [44,45].

Event schemata are cognitive scripts that describe the sequential organization of events in everyday social activities [46,47]. They provide the basis for anticipating the future, setting goals, making plans and comprehending the mental states and intentions of other individuals in social interactions. It can be demonstrated that a broad range of social tasks such as social judgment about (i) event knowledge, (ii) morality, (iii) social scripts and (iv) theory of mind beliefs elicit activation in the mPFC (Figure 2a) [25]. These task activation patterns in the mPFC can be parsimoniously explained by reenactment of different elator components contained within event schemata: the event knowledge tasks draw on goals or end-states of agents or actions; the morality tasks on just or unjust actions of agents; the social script tasks on the sequence of actions
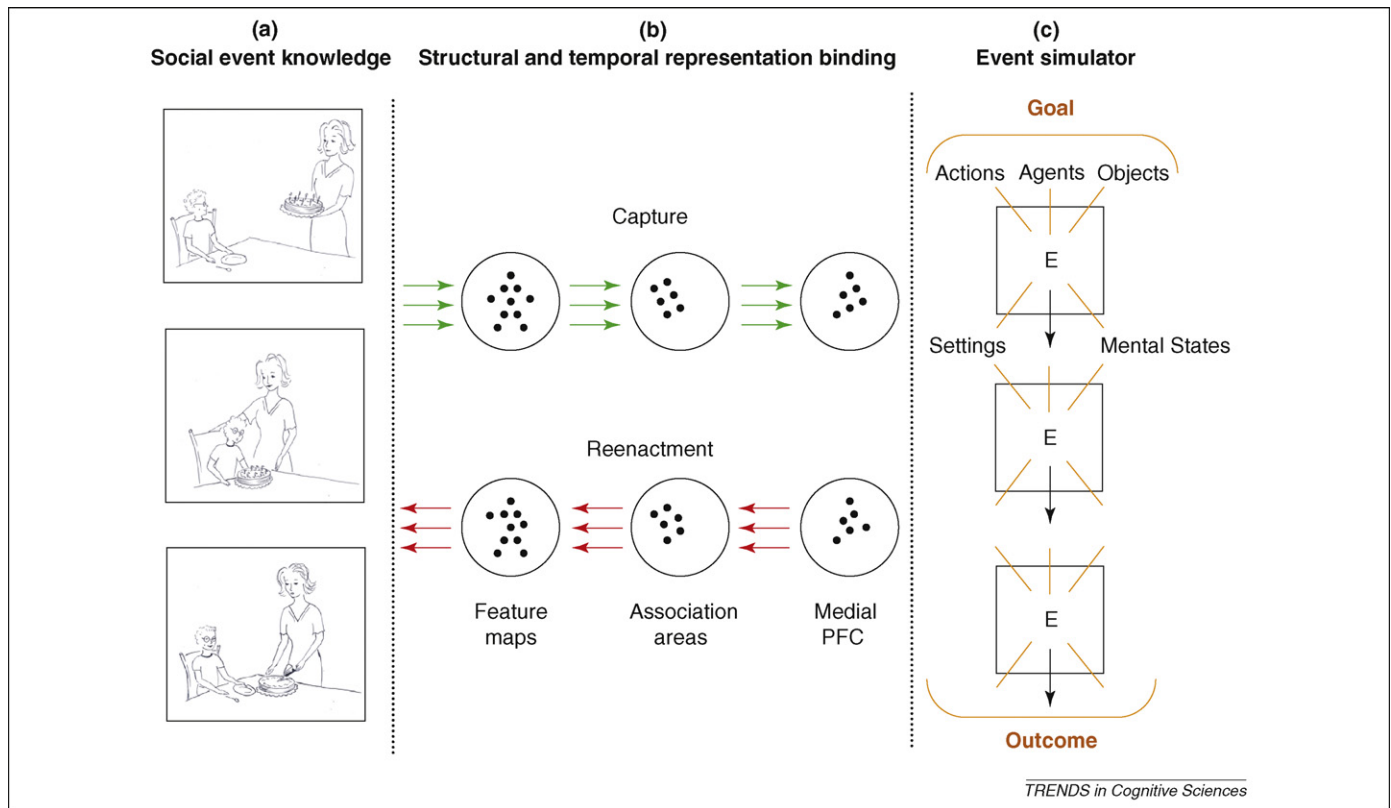
Figure 1. STRing theory, elators and elations. **(a)** Social event knowledge. The abstraction for 'hosting a birthday party' represents a sequence of events (e.g. the host invites guests to the birthday party, bakes a cake, lights the candles, presents the cake to the birthday boy, sings 'happy birthday') that involved agents (e.g. host and birthday boy), actions (e.g. baking a cake and lighting the candles), objects (e.g. birthday cake and candles), mental states (e.g. joy and happiness) and background settings (e.g. dining room). **(b)** Structural and temporal representation binding. Capture: feature detectors in relevant modalities of the brain capture modality-specific states, whereas nearby association areas store the patterns' features to represent aspects of experience. The mPFC conjoins patterns of activation across association areas and time, capturing the semantically structured and temporally organized components of social event knowledge into an elator. Reenactment: once an elator exists, it can reenact small subsets of its content as specific elations. In particular, a subset of neurons in the mPFC can reactivate elator components in the absence of bottom-up sensory stimulation, and inferences about the situation can be drawn via pattern completion with all components simulated. The reenactment of elator content arises through structural and temporal representation binding that encompasses a multi-modal representation distributed throughout the brain's association and modality-specific areas. **(c)** Elator. Elators are semantically structured by events that are defined by distinctive features such as agents, actions, objects, mental states and settings, and temporally organized on the basis of goals enabling the selection of goal-directed event sequences and event outcomes enabling the selection of the affective responses and reward values associated with goal achievement.

and the theory of mind beliefs tasks on mental states of agents.

Because elators provide the capacity to interpret the behaviors of individuals over a long period of time under multiple circumstances to recognize the common goal in these behaviors, they provide the underlying cognitive structure for the development of traits represented in person and self schemata. On the one hand, we claim that goal knowledge about an elator enables inferences about the likely actions of agents and, hence, is essential for the development of person schemata. Person schemata deal with abstracted conceptual structures of personality traits that enable a person to categorize and make inferences from the experiences of interactions with other people, and to anticipate the nature of interactions with individuals by providing control and predictability in social interactions [48]. On the other hand, we argue that outcome knowledge about an elator supports inferences about the likely affective response and reward values that result from goal achievement for the self, and hence, is essential for the development of self schemata. Self schemata refer to cognitive generalizations about the self derived from past experience that organize and guide the processing of

self-related information contained in the individual's social experience [49].

Segregation of elator functions

We emphasize the idea for a segregation of elator functions along the continuum of the dorso-ventral mPFC axis based on its connectivity with posterior and subcortical brain regions (Figure 3) [50–52]. According to the STRing theory, goal knowledge about an elator supports inferences about the person schemata and preferentially recruits the dmPFC. This 'goal pathway' has reciprocal connections with brain regions that are associated with motor control (premotor cortex and supplementary motor area), performance monitoring (cingulate cortex) and higher-order sensory processing (association areas and parietal cortex) [52], and is therefore well suited to support inferences about the likely actions performed by agents for goal achievement. By contrast, outcome knowledge about an elator enables inferences about the self schemata and preferentially recruits the vmPFC and/or mOFC. This 'outcome pathway' has reciprocal connections with brain regions that are associated with emotional processing (amygdala), memory (hippocampus), reward processing
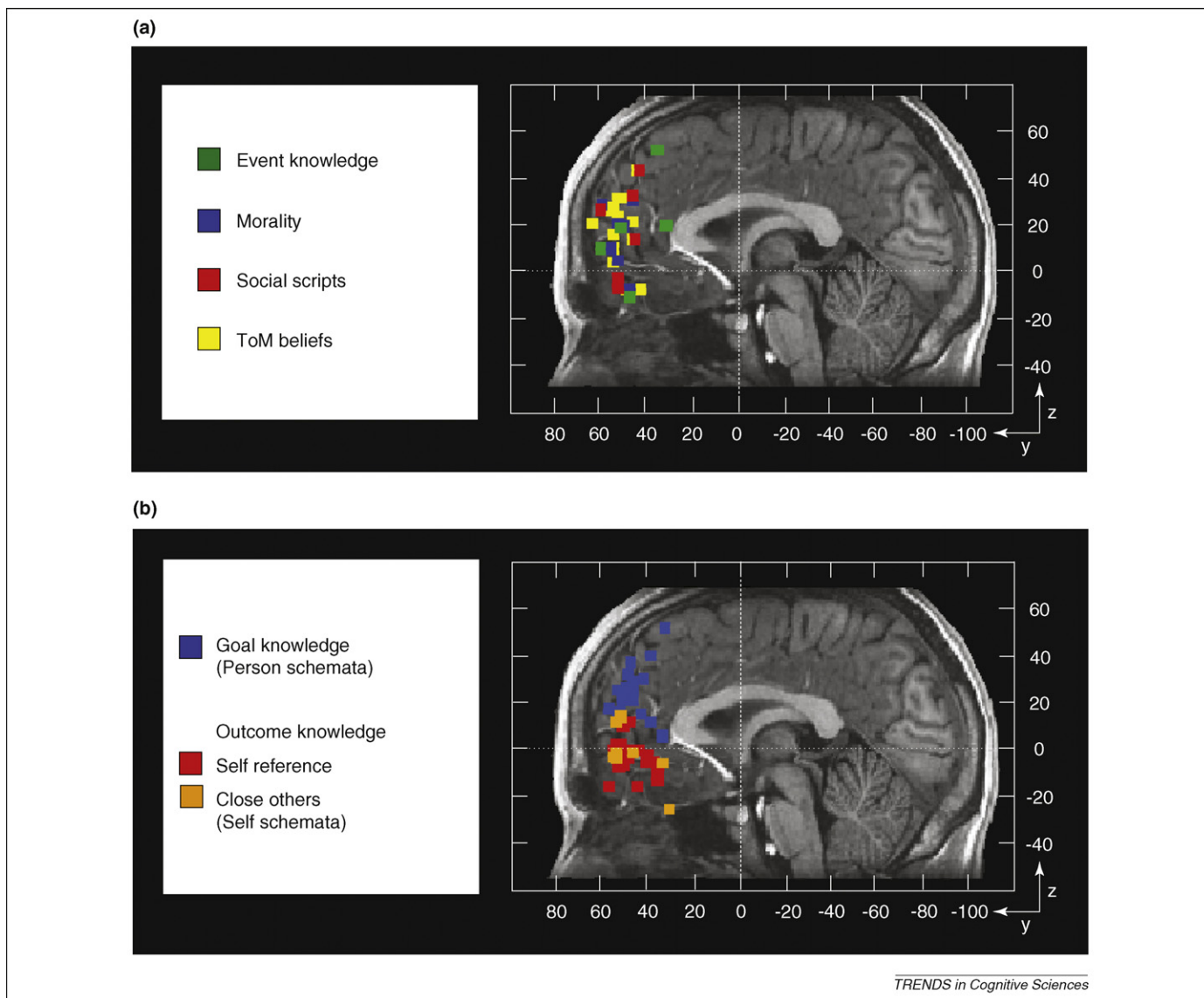
Figure 2. Neuroscience evidence in support for elators. **(a)** Event schemata. Functional neuroimaging meta-analysis results are displayed for social judgment tasks about event knowledge, morality, social scripts and theory of mind (ToM) beliefs. Tasks reenacted elator components contained within event schemata and elicit activation in the mPFC. **(b)** Person and self schemata. Functional neuroimaging meta-analysis results are displayed for tasks that reenact elator components contained within person and self schemata. Goal knowledge supports inferences about person schemata and preferentially recruits the dorsal part of mPFC. Outcomes knowledge enables inferences about self schemata and preferentially recruits the ventral part of the mPFC. Adapted, with permission, from Ref. [25]. Talairach space: *y*-axis (anterior-posterior) and *z*-axis (inferior-superior).

(basal ganglia including the striatum and the nucleus accumbens) and higher-order sensory processing (temporal visual association areas) [52], and is therefore well suited to enable inferences about the likely affective and reward value accompanying goal achievement. Note that it is not by chance that affect and reward are regarded as key components for self schemata. Anatomically, the 'core self' has been associated with the vmPFC and/or mOFC [53,54] because affect and reward are crucial to guide efficiently an individual's decision-making during social conduct [55,56].

The proposed segregation of elator functions is supported by a recent quantitative neuroimaging meta-analysis [25] (Figure 2b). The results demonstrated that inferences about the person schemata – individuals made judgments about goal knowledge that enables an inference about the goal-directed actions of others derived from

behavior in short stories, sentences and single words, or interactive neuroeconomic games – preferentially activated the dmPFC. In contrast, inferences about the self schemata – individuals made judgments about event outcomes that enables an inference about the affective states and rewards associated with goal achievement in retrospective to oneself or close others (e.g. mother and relative friends) in the form of ratings and descriptions, memories about the self and thinking about one's hopes – preferentially activated the vmPFC and/or mOFC. In addition, there is evidence that damage to the dmPFC leads to an inability to set goals, make plans and comprehended the mental states of others in social interactions [57], whereas damage to the vmPFC and/or mOFC leads to an inability to develop a coherent model of one's own self with subsequent emotional lability [58,59] and to severe impairment of social behavior such as social inappropriateness, lack of
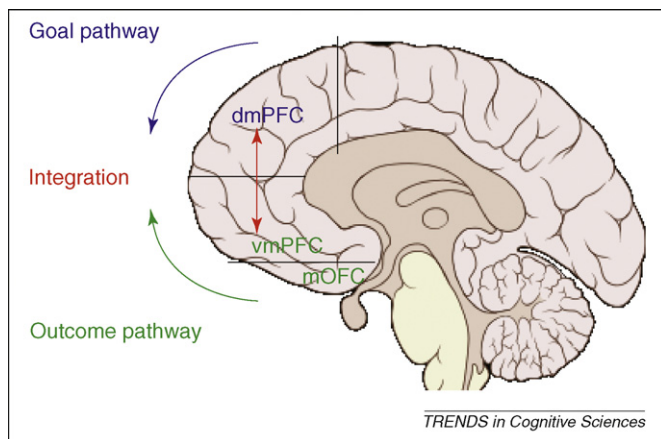
Figure 3. mPFC and elator functions. The mPFC consists of three sectors: medial orbital frontal cortex (mOFC; z<-15 mm of the Talairach atlas), ventral mPFC (vmPFC; z<20 mm) and dorsal mPFC (dmPFC; z≥20 mm). The anterior part of the cingulate cortex is included in the mPFC for convenience throughout the article. The goal knowledge pathway in the dmPFC supports inferences about the likely actions performed by agents for goal achievement. The outcome knowledge pathway in the vmPFC and/or mOFC enables inferences about the likely affective response and reward value accompanying goal achievement. Most rostral parts of the mPFC mediate hierarchically organized elators that allow integration of information from the goal pathway with information from the outcome pathway.

insight and initiative, poor judgment and inappropriate affect [60–63].

Note that event, person and self schemata are not represented independently in the mPFC; they are simulations of underlying elators with different components being differentially weighted depending on the nature of social conduct. In addition, different elator components can be intimately involved in both planning and monitoring one's own behavior in addition to understanding and predicting the behavior of others. For example, theory of mind beliefs that rely on goal knowledge (i.e. inferences about the likely actions performed by agents for goal achievement) will preferentially elicit activation in the dmPFC, whereas theory of mind beliefs that rely on outcome knowledge (i.e. inferences about the likely affective and reward value accompanying goal achievement) will preferentially elicit activation in the vmPFC (Figure 2a). Consequently, elators can be seen as shared representations that have the capacity to coordinate first-person and third-person information via a single conceptual system.

Importantly, as one moves more rostrally in the mPFC, progressively more general elators are represented, which are hierarchically organized and guide social behavior over progressively longer temporal intervals. The hierarchical structure of elators maps directly onto the anatomical hierarchical architecture of the mPFC [18,21,64]. Because the most rostral part of the mPFC (Brodmann's area 10) is one of the last brain regions to mature [65], it is ideally suited to represent more general elators that integrate information from the goal pathway with information from the outcome pathway. A recent functional neuroimaging study provides evidence for such a rostro-caudal gradient in the mPFC [29] (Box 3).

Conclusion

Based on the biology, structure and function of the mPFC, we developed an integrative theory of the cognitive and neural bases of social event knowledge. The STRing theory

Box 3. Rostro-caudal gradient for social event knowledge in the mPFC

An economy of representation develops as social event knowledge becomes more frequently used. A recent functional neuroimaging study provided evidence for a rostro-caudal gradient in the mPFC based on how often social scripts were reportedly performed in daily life [29]. Functional magnetic resonance imaging was applied while healthy volunteers were engaged in event order judgments about the sequential organization of low- (e.g. going to a funeral), moderate- (e.g. going bowling), and high-frequency (e.g. going out for dinner) social scripts. After presenting the goal of the script (e.g. going out for dinner) and a pair of events (e.g. look at menu – order dinner), individuals were asked to judge whether the pair of events was correctly ordered. The results demonstrated that subregions of the mPFC (Brodmann's area [BA] 10) were differentially engaged in mediating social scripts depending on how often they were reportedly performed in daily life. The posterior medial part of BA 10 (labeled as 'post MPFC' in Figure I) was activated for high-frequency social scripts, which indicate that it encodes sparser information about its goal-directed action sequences and event outcomes (Figure I). By contrast, the anterior medial part of BA 10 (labeled as 'ant MPFC' in Figure I) was activated for low-frequency social scripts, which indicates that it encodes more dense information about its goal-directed action sequences and event outcomes. Interestingly, each of the frequency-dependent mPFC regions falls onto one of the three architectonic subdivisions of the human BA 10 [52]. These subregions have a similar cellular pattern, but vary in the degree of granularity and the development of cortical layer III (and layer IV), with the most prominent and well-developed layer III located in the polar area, which is not observed in non-human primates [70]. This architectural complexity increase along the medial axis towards the frontopolar cortex might be an indication of the underlying frequency-dependent representation of social event knowledge encoded in each of the medial subregions.
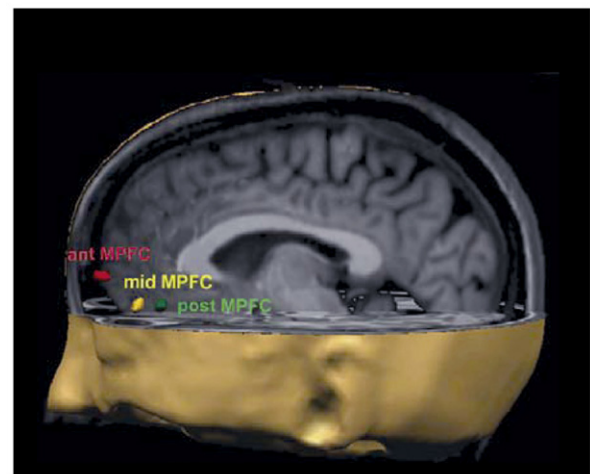

Figure I. Rostro-caudal gradient for social event knowledge in the mPFC. Adapted, with permission, from Ref. [29].

assumes that the mPFC represents elators that encompass a multi-modal representation of social event knowledge distributed throughout the brain's association and modality-specific areas. Once an elator exists, it can reenact small subsets of its content as specific elations. Elators as abstract dynamic structured summary representations provide the underlying properties for social cognitive structures such as event schemata, person schemata and self schemata that are intimately involved in planning and monitoring one's own behavior in addition to under-

Box 4. Outstanding questions

- How is social event knowledge involved in remembering the past (autobiographic memory) and imagining the future (prospective memory)?
- Research has shown that the central goal for social event knowledge changes with age. For example, for the 'hosting a birthday party' script, younger children tend to organize their social scripts around more object-centered actions (e.g. blowing out the candles), whereas older children include more socially centered actions (e.g. inviting the guests). How is this change reflected in the neural architecture of the maturing brain?
- The mPFC has been described as one of the crucial regions in the 'default system', which is 'activated' during rest and 'deactivated' during cognitively effortful tasks. Because there is an overlap between the mPFC typically involved in social cognition and the 'default system', what is the role of social event knowledge in the 'default system'?
- How does social event knowledge shape the development of belief systems ranging from moral decision making to the practice of religion?
- Given the fact that the left PFC is more adept at constructing determinate, precise and unambiguous representations of the world, whereas the right PFC is more adept at constructing and maintaining fluid, indeterminate, vague and ambiguous representations of the world, what is the role of social event knowledge within the left and right hemisphere?

standing and predicting the behavior of others. Consistent with neuroscience evidence, we proposed a segregation of elator functions along the dorso-ventral mPFC axis: goal knowledge mediated by the dmPFC pathway supports inferences about the likely actions performed by agents for goal achievement, whereas outcome knowledge mediated by the vmPFC and mOFC pathway supports inferences about the likely affective and reward value accompanying goal achievement. Most rostral parts of the mPFC mediate hierarchically organized elators that allow integration over progressively longer temporal intervals of information from the goal pathway with information from the outcome pathway. The STRing theory generates testable hypotheses, specifies anatomically and functionally the nature of the information being processed, and poses new questions for empirical research (Box 4). From our perspective, studying the nature of dynamic structured summary representations is a fruitful way to characterize and identify the neural basis of social cognition. Defining social dimensions that can be reconciled with the brain's anatomical and physiological properties can bring us one step closer to an understanding of the contribution of the PFC to uniquely human social behavior.

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