

Chapter 7

Hierarchical Organization of Frontoparietal Control Networks Underlying Goal-Directed Behavior

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Abstract Goal-directed behavior involves a variety of processes that operate over different temporal scales, from the generation and maintenance of distal (long-term) goals to the identification of proximal (immediate) subgoals to the execution of actions in service of those goals. There is also evidence suggesting that the neural underpinnings of goal-directed behavior may be organized along a hierarchical anterior-to-posterior gradient, at least within the frontal cortex. In this review, we examine recently identified large-scale functional networks that are composed of regions spanning the frontal, parietal, and lateral temporal cortices and determine whether there is evidence of a hierarchical organization based on the representation of goals at different temporal scales. Findings from recent functional neuroimaging studies suggest that: (1) the anterior frontoparietal network is involved in generating and planning for distal goals, (2) the posterior frontoparietal is involved in realizing proximal goals by representing desired outcomes and currently relevant rules for action, and (3) the sensorimotor network translates such rules into the execution of motor output. These findings are consistent with the idea that goal-directed behavior can be deconstructed into a temporal hierarchy of goals and corresponding brain networks.

Keywords Goals • Prefrontal • Control • Frontoparietal network • fmri • Rewards • Rules

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7.1 Introduction

Goal-directed behavior involves a variety of processes that operate over different temporal scales. Much of human behavior is guided by *distal* (long-term) goals, including those related to career and family aspirations. For example, based on one's personal preferences and skills, a young adult may decide to become a doctor. To realize such distal goals, it is often necessary to identify and carry out numerous *proximal* (immediate) goals. For example, to become a doctor, the individual will need to study for classes, complete clinical internships, take steps to become licensed, etc. These proximal goals guide much of day-to-day behavior and often require the use of instructions or rules to direct action in a goal-congruent manner. Finally, at the shortest temporal scale, proximal goals need to be translated into the execution of specific actions (e.g., opening a text book and taking notes). This requires the translation of proximal goals and rules for action into corresponding motor commands. As this example illustrates, many instances of goal-directed behavior may emerge as the result of a temporal hierarchy of goals.

Considerable research using humans, nonhuman primates, and rodents has sought to characterize the critical neural substrates of goal-directed behavior. Regions of the lateral prefrontal, posterior parietal, and lateral temporal cortices have been linked to various aspects of goal-directed behavior including rule use, working memory, reasoning, planning, abstract thinking, and response inhibition (Aron et al. 2004; Badre and D'Esposito 2007; Bunge 2004; Bunge et al. 2003; Christoff and Gabrieli 2000; Christoff et al. 2009a; Cole and Schneider 2007; Dixon and Christoff 2012; Dosenbach et al. 2006; Duncan 2001, 2010; Koechlin et al. 2003; Kounieher et al. 2009; Miller and Cohen 2001; Petrides 2005; Rushworth et al. 2007). Furthermore, recent studies suggest that these regions also integrate information about reward and punishment (Beck et al. 2010; Dixon 2015; Dixon and Christoff 2012, 2014; Dixon et al. 2014a; Histed et al. 2009; Jimura et al. 2010; Kobayashi et al. 2006; Padmala and Pessoa 2011; Pochon et al. 2002; Watanabe 1996).

Accumulating evidence suggests that the goal-directed action is instantiated along a hierarchical anterior-to-posterior gradient, at least in the frontal cortex. Generally speaking, more anterior regions have been linked to temporally extended and abstract action goals, while more posterior regions have been linked to concrete information that governs immediate motor output (Badre and D'Esposito 2009a; Bunge and Zelazo 2006; Christoff and Gabrieli 2000; Christoff et al. 2009a; Dixon 2015; Dixon et al. 2014a; Koechlin et al. 2003; Petrides 2005). However, while most of this research has focused on establishing associations between the activity of localized brain regions and specific cognitive functions, ultimately, regions of the frontal cortex operate in concert with parietal and temporal cortices as coordinated large-scale functional networks (Fox and Raichle 2007; Power et al. 2011; Smith et al. 2013; van den Heuvel and Hulshoff Pol 2010; Yeo et al. 2011). This leads to the possibility that there may be a hierarchical organization of functional brain networks that underlies goal-directed action. The literature provides some

evidence consistent with this possibility; however, it has yet to be integrated into a coherent framework.

In this review, we examine three functional networks consisting of frontal, parietal, and temporal cortices and identify their roles in goal-directed behavior. We begin by reviewing the basic elements of functional connectivity analyses. Next, we examine the function of each network, in turn, by summarizing findings from recent functional magnetic resonance imaging (fMRI) studies. This review suggests that the functions of the three networks correspond remarkably well with the idea of a temporal hierarchy of goals.

7.2 Functional Connectivity Networks

The last decade has seen tremendous progress in understanding the way in which brain regions group together as meaningful systems or networks. Much of this work has emerged from functional connectivity (FC) analyses, which offer a powerful, non-invasive tool for delineating the functional architecture of the human brain. FC analyses typically involve computing the correlation between temporal fluctuations in blood oxygenation level-dependent (BOLD) signal across distributed brain regions (Biswal et al. 1995; Fox et al. 2005; Greicius et al. 2003; Power et al. 2011; Smith et al. 2009; Yeo et al. 2011). These analyses have repeatedly shown that a given brain region will exhibit correlated activation with a very specific collection of other regions, consistent with the idea that they work together as a functional system. For the most part, FC analyses have been performed on data acquired during the “resting state,” with the idea that spontaneous fluctuations in activation provide a window into the *intrinsic* neurocognitive architecture of the brain (Biswal et al. 1995; Fox and Raichle 2007; Greicius et al. 2003). A multitude of distinct functional networks have been identified, with each being associated with a specific cognitive function (e.g., visual processing, language, somatosensory-motor control, attention) (Biswal et al. 1995; Buckner et al. 2009; Dosenbach et al. 2007; Fair et al. 2008; Fox et al. 2006; Greicius et al. 2003; Smith et al. 2009; Vincent et al. 2007, 2008). The validity of the networks identified by FC is supported by the fact that they exhibit relative stability across time and context (Damoiseaux et al. 2006; Smith et al. 2009; Zuo et al. 2010) and bear a close resemblance to known anatomical connectivity patterns (Honey et al. 2009; Margulies et al. 2009; Raichle 2009; van den Heuvel and Hulshoff Pol 2010; Van Dijk et al. 2010).

A recent FC-based parcellation using the data of 1000 participants revealed that regions of the frontal, parietal, and temporal cortices cluster into multiple distinct networks (Yeo et al. 2011). This functional organization is important to consider when trying to make links between neural substrates and the different levels of cognitive processing involved in goal-directed behavior. The present discussion will focus on three of the networks identified by Yeo et al. (2011), which we refer to as: (1) the anterior frontoparietal network (aFPN), (2) the posterior frontoparietal

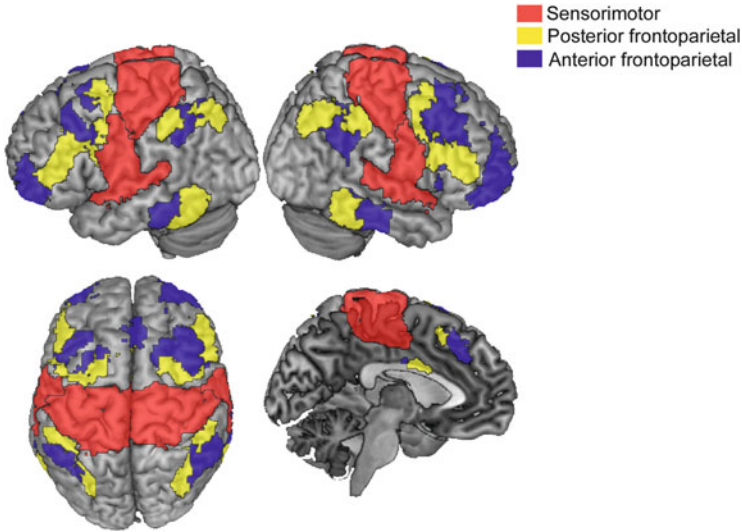


Fig. 7.1 Frontoparietal networks defined based on patterns of functional connectivity (Adapted from Yeo et al. 2011). Sensorimotor network (*red*), posterior frontoparietal network (*yellow*), anterior frontoparietal network (*blue*)

network (pFPN), and (3) the sensorimotor network (SMN) (Fig. 7.1). These networks are organized along a roughly anterior-to-posterior gradient, particularly in the frontal cortex. Below, we review findings pertaining to the function of each network and demonstrate that they map closely to the different elements of goal-directed behavior described above. This suggests that these networks may reflect a hierarchical organization of cognitive processes that operate over different time scales.

7.3 The Anterior Frontoparietal Network and Distal Goals

The aFPN is exclusively comprised of higher-order multimodal association areas in the frontal, parietal, and lateral temporal cortex (Spreng et al. 2010; Vincent et al. 2008; Yeo et al. 2011). Theories have linked regions of the aFPN to complex, internally oriented cognitive processes (Burgess et al. 2007; Christoff and Gabrieli 2000; Ramnani and Owen 2004a) based on its activation across diverse tasks, including complex reasoning (Bunge et al. 2005; Christoff et al. 2001; Kroger et al. 2002; Monti et al. 2007), memory retrieval (Rugg and Wilding 2000; Velanova et al. 2003), multitasking (Braver and Bongiolatti 2002; Koechlin et al. 1999), moral decision-making (Greene et al. 2004), abstract thought (Badre and D’Esposito 2009b; Christoff et al. 2009b), spontaneous thought (Christoff et al. 2009a; Christoff et al. 2004b), and future-oriented reward processing (Diekhof and

Gruber 2010; Jimura et al. 2013; McClure et al. 2004). Specifically, the aFPN appears to be involved in a reflective or monitoring function that coordinates, integrates, and evaluates the outputs of prior stages of cognitive processing (Christoff and Gabrieli 2000; Fletcher and Henson 2001; Petrides 2005; Ramnani and Owen 2004b; Tsujimoto et al. 2010). Consistent with this, recent work employing subjective reports and well-controlled paradigms has shown that this network, especially the rostrolateral prefrontal cortex (RLPFC), is critical for *metacognitive awareness*—the ability to reflect on and accurately report one’s mental contents (Baird et al. 2013; De Martino et al. 2013; Fleming et al. 2010; McCaig et al. 2011; McCurdy et al. 2013). For example, we have shown that participants can learn to modulate RLPFC activation by monitoring real-time feedback and directing attention to their thoughts (McCaig et al. 2011).

Consistent with a role in reflecting on thoughts and feelings, the aFPN is often coactivated with the default mode network (DMN), which has a well-established role in internally directed self-referential processes (Andrews-Hanna et al. 2010; Buckner et al. 2008; Christoff et al. 2009b; Fox et al. 2005; Gusnard and Raichle 2001; Mazoyer et al. 2001; Shulman et al. 1997). Furthermore, resting-state functional connectivity analysis has revealed extensive functional interactions between regions of the aFPN and DMN (Spreng et al. 2013). These networks are activated during periods of waking rest and boring tasks, when individuals tend to reflect on personal concerns and future plans, especially those involving social relationships (Andrews-Hanna 2012; Andrews-Hanna et al. 2010; Fox et al. 2013; Klinger 2008; Mar et al. 2012; Christoff et al. 2004a, 2009b; Fox et al. 2015).

Thus, the aFPN and its interaction with the DMN may enable individuals to transcend the allure of immediate sensory input and, instead, allow attention to be directed to an internal train of thought (Dixon et al. 2014b). One function of internal thought may be to discern long-term goals and plans to achieve them. In one study, Spreng et al. (2010) had participants think about personal future goals (e.g., academic success) and three to five steps necessary to achieve those goals and obstacles that might interfere with goal attainment. They monitored fMRI signal while participants engaged in this autobiographical planning task, and compared it to signal during a control task that did not require keeping in mind a distal goal or means to achieve it. The results demonstrated robust activation of the aFPN and DMN as participants engaged in future goal planning (Spreng et al. 2010). These findings are consistent with the idea that interactions between the aFPN and DMN enable individuals to internally simulate future scenarios and intermediary steps necessary to turn those scenarios into reality. In another study, we had participants perform a task requiring a series of goal-directed actions and informed them that they could earn up to \$60 at the end of the experiment based on their performance (Dixon et al. 2014a). Participants had to use rules to respond to visual images on each trial, and following their response, they were presented with a feedback screen that revealed their total cumulative winnings up to that point. Thus, the feedback screen allowed participants to monitor their progress toward the distal goal of earning \$60. The results demonstrated robust activation of the aFPN specifically

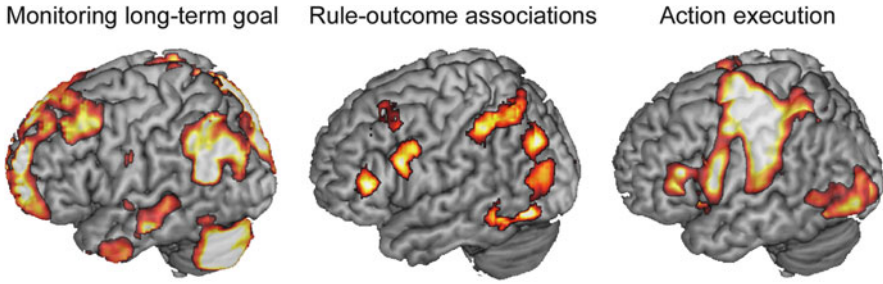


Fig. 7.2 Hierarchical organization of functional networks (Results adapted from Dixon and Christoff (2012) and Dixon et al. (2014a)). The aFPN is specifically activated when individuals generate and monitor progress toward distal goals. The pFPN is involved in guiding behavior toward proximal goals by specifying currently relevant rule-outcome associations. The SMN is selectively activated during the execution of overt actions

during this task phase, when information about progress toward the distal goal was available (Fig. 7.2) (Dixon et al. 2014a).

Corroborating these findings, regions within the aFPN are recruited when individuals plan steps to attain a future goal (Gerlach et al. 2014), choose to avoid situations that may interfere with the attainment of future rewards (Crockett et al. 2013), and select actions directed toward future rather than immediate rewards (Diekhof and Gruber 2010; Jimura et al. 2013; McClure et al. 2004). Furthermore, several studies have found that the aFPN is critical for the coordination of multiple subgoals (Braver and Bongiolatti 2002; Dreher et al. 2008; Koechlin et al. 1999). Finally, the aFPN plays an important role when individuals decide to shift from current actions to explore new options that may yield better long-term outcomes (Badre et al. 2012; Boorman et al. 2009) suggesting that it may be involved in prioritizing motivational goals (Dixon and Christoff 2014). The involvement of the aFPN in generating distal goals and steps to achieve them is consistent with its activation in reasoning tasks that require the capacity to see the relationships between multiple pieces of information (Bunge et al. 2005; Christoff et al. 2001; Kroger et al. 2002; Monti et al. 2007) and the suggestion that regions of the aFPN supports the serial organization of several subgoals (Koechlin et al. 1999) and the manipulation and evaluation of internally generated information (Christoff and Gabrieli 2000).

To summarize, the findings reviewed above are consistent with the idea that the aFPN is preferentially involved in processes related to distal rather than proximal goals. The aFPN has a close relationship with the DMN and is consistently recruited when individuals direct attention internally to thoughts about personal concerns and steps to achieve desired future outcomes. Thus, the aFPN may sit at the top of the hierarchy supporting goal-directed behavior.

7.4 The Posterior Frontoparietal Network and Proximal Goals

Whereas the aFPN plays a role in discerning overarching priorities, the pFPN operates on a shorter time scale, contributing to the attainment of proximal goals. The pFPN is not required for all proximal goals; rather, it is primarily recruited when desired outcomes can only be obtained through the intentional regulation of behavior, often referred to as exerting *cognitive control*. A large literature has shown that the pFPN is invariably engaged by experimental tasks that involve responding to externally presented stimuli (Duncan 2010). The regions comprising this network include frontal, parietal, and lateral temporal regions that are each located posterior to the regions comprising the aFPN. This network facilitates goal-directed behavior by encoding and maintaining task rules within working memory (Bunge et al. 2003; De Baene et al. 2012). Rules often take the form of “if-then” mappings that specify a set of stimulus-response contingencies.

Recent work has shown that individuals are reluctant to employ cognitive control due to an inherent *effort cost* (Botvinick and Braver 2015; Dixon and Christoff 2012; McGuire and Botvinick 2010). For example, when given the choice between two tasks, individuals will reliably choose the easier task (McGuire and Botvinick 2010). It requires considerable effort to intentionally direct action, and this may often be experienced as aversive. Accordingly, individuals only engage of cognitive control if they think that it will produce an emotionally valuable outcome that outweighs the effort cost (Dixon and Christoff 2012). We have reported that when given the choice between selecting a well-practiced habitual action or a rule-based action that requires cognitive control, individuals are only likely to select the latter option if it is expected to result in a larger monetary reward than the habitual action (Dixon and Christoff 2012). This implies that many moment-to-moment decisions about goal-directed behavior require that individuals perceive the relationship between cognitive demands (e.g., rule use) and desired outcomes.

We have found evidence that the pFPN encodes such rule-outcome associations (Dixon and Christoff 2012). Participants performed a task in which they employed simple rules to obtain monetary rewards. There were two different rules (judge whether a face is male/female or judge whether a word has a concrete/abstract meaning) and two different monetary outcomes (25¢ or \$0). Importantly, each trial started with an instruction cue that signaled the currently relevant rule and which outcome to expect. On some trials, a second instruction cue appeared prior to the stimulus and signaled either the same (repeated) rules or novel rules and either the same (repeated) outcome or a novel outcome. This 2×2 factorial design allowed us to look for fMRI adaptation (i.e., a change in neural activation) when there was repetition of the rules, repetition of the reward outcome, or repetition of a specific rule-outcome pairing. Several areas within the pFPN exhibited an interaction effect, demonstrating fMRI adaptation specifically when there was repetition of a specific rule-outcome pairing, but not when there was repetition of just the rules or just the outcome (Fig. 7.2). Hence, this network represents the *association* between a

specific rule and an expected motivational outcome (Dixon and Christoff 2012). Given that rule-outcome combinations changed from trial to trial, this suggests that the pFPN has the capacity to rapidly represent rule-outcome associations based on symbolic instructed information and thereby contribute to the acquisition of proximal goals.

Consistent with our findings, recent evidence indicates that activation of the inferior frontal sulcus—a key node of the pFPN—reflects an interaction between the complexity of rules that are required to respond to stimuli and the size of an expected reward outcome (Bahlmann et al. 2015). Moreover, a study employing multivariate pattern analysis found that several regions of the pFPN exhibited stronger encoding of task rules during a monetary incentive condition relative to the no incentive condition (Etzel et al. 2015). Similarly, Jimura et al. (2010) found that monetary incentives shifted pFPN working memory-related activation toward a sustained pattern indicative of enhanced proactive control (i.e., anticipatory maintenance of task information). Together, these studies indicate that the pFPN integrates cognitive demands and reward outcomes and thereby represents information that is crucial in guiding action toward proximal goals.

The majority of studies to date have focused on the engagement of cognitive control in service of obtaining an immediately available incentive. However, in many real-life situations, cognitive control may be required to complete numerous tasks in service of a distal goal, without immediate reinforcement. In fact, to attain distal goals, it is often necessary to resist the temptation of immediate rewards that may interfere with proximal goals that support the attainment of distal goals (e.g., choosing to stay in and study for an exam instead of going out to the movies). In these cases, input from the aFPN signaling the value of the distal goal may engage the cognitive control processes of the pFPN such that relevant proximal goals are completed, and the aFPN may simultaneously send inhibitory signals to regions such as the ventral striatum that are sensitive to immediate rewards. Findings from delay of gratification paradigms appear to support this idea (Diekhof and Gruber 2010; Jimura et al. 2013; McClure et al. 2004; van den Bos et al. 2014); however, more research is needed that directly examines situations in which the aFPN and pFPN may be in a hierarchical relationship, contributing to the same goal at different levels (temporal scales).

To summarize, the pFPN is involved in specifying proximal goals and how to achieve them. This network is invariably activated in studies that require focused attention on externally presented stimuli, and it represents rule-outcome relationships that guide action selection in a goal-congruent manner. In doing so, the pFPN may exert top-down control over sensorimotor regions that execute actions. In many cases, the pFPN may serve as the second tier of the goal hierarchy, taking information from the aFPN about distal goals and translating this information into corresponding proximal goals.

7.5 The Sensorimotor Network and the Execution of Goal-Directed Actions

Once the pFPN has established a proximal goal and the rules specifying goal-appropriate behavior, this information needs to be translated into the execution of specific voluntary actions. The SMN supports this process (Bunge 2004; Koehlin et al. 2003; Petrides 2005). The SMN is a set of interconnected brain regions that serve to integrate concrete sensory and motor information for the initiation of voluntary movement. The main constituents of this network have had a long history of study in neuroscience (Ferrier 1873; Penfield and Boldrey 1937). Resting-state functional connectivity studies have revealed that the SMN consists of primary motor and somatosensory cortices, as well as lateral and medial premotor regions (Biswal et al. 1995; De Luca et al. 2005; Power et al. 2011; Xiong et al. 1999; Yeo et al. 2011).

The primary and premotor cortices, as their names suggest, mediate motor sequences. Historically, research has viewed these regions as in a hierarchical relationship with each other, with the premotor cortex concerned with complex higher-order movements and primary motor cortex concerned with breaking these movements down into their basic constituents to allow for execution (Picard and Strick 1996; Rizzolatti and Luppino 2001). Specifically, the premotor cortex consists of a number of specialized subregions which correspond to different high-level functions such as the planning, preparing, or imagining of movement (Muakkassa and Strick 1979; Rizzolatti et al. 1988, 2002). Petrides (2005) found that lesions to the macaque premotor cortex caused selective impairments in performance on visuomotor conditional learning tasks, which involve learning associations between visual stimuli and movement sequences (Petrides 2005). Thus, the premotor cortex is vital for the ability to translate visual information into correct motor responses. It seems likely that the premotor cortex uses information about task rules represented by the pFPN to discern goal-appropriate actions (Bunge 2004; Koehlin et al. 2003).

In comparison, the primary motor cortex contains a body map, with different sectors linked to the control of specific groups of muscles or body parts (Grafton et al. 1991; Penfield and Boldrey 1937). As such, it has typically been viewed as a slave to the commands of the premotor cortex, responsible for translating action commands into sequences of muscle recruitment. Recent work, however, has suggested that this may be an overly simplistic view. Originating from the finding that complex behavioral sequences could be evoked through stimulation of primary motor subregions (Graziano et al. 2002), multiple lines of research have suggested that the primary motor cortex additionally contains a map of ethologically meaningful action sequences (Graziano 2006, 2016). For example, electrical stimulation of certain regions of primary motor cortex in primates has been demonstrated to reliably evoke sequences such as eating-related hand to mouth movements or tree-climbing movements (Graziano 2016). While the exact functional relationship

between the primary and premotor cortices is still under debate, both are central for the execution of voluntary movement.

The primary somatosensory cortex is associated with the conscious sense of touch, including feelings of pressure, temperature, vibration, position, and movement that arise from the skin, joints, and muscles. It contains a somatotopic map of the body, with greater cortical surface area being devoted to areas possessing greater tactile sensitivity, and this has been pictorially rendered in the so-called sensory homunculus (Penfield and Boldrey 1937). The coordinated interaction between primary and premotor cortices on the one hand, and somatosensory cortex on the other hand, may contribute to an embodied sense of self and agency (Christoff et al. 2011). When performing an action, a copy of the motor commands can be compared with the resulting changes in sensory input by a comparator mechanism (likely instantiated by the SMN), to implicitly signal that one has acted upon the world (Christoff et al. 2011). “Reafferent” sensory signals that match initiated motor commands are self-specific, as they are intrinsically related to agent’s executed action, whereas all other sensory changes are nonself-specific (Christoff et al. 2011). Thus, by tracking the relationship between efferent motor signals and afferent sensory consequences, the SMN may contribute to the bodily experience of agency associated with the expression of goal-directed behavior.

The aforementioned findings suggest that the SMN is involved in processes that are closely related to the actual initiation of goal-directed actions and not other high-level processes. We recently found evidence consistent with this idea. We analyzed neural activation during several distinct phases of a cognitive task: (1) instruction cue period, during which the relevant rules and outcome for the current trial were indicated; (2) delay period, which required working memory; (3) stimulus-response period during which participants executed an action; and (4) feedback period. We found that medial and lateral premotor regions were preferentially activated during the stimulus-response period, when participants executed an overt goal-directed action (Fig. 7.2) (Dixon et al. 2014a). This suggests that the SMN mainly contributes to goal-directed action at the finest temporal scale, when goals are realized through embodied action output.

To summarize, the SMN has been associated with specifying movement plans and monitoring reafferent feedback that can be used to fine-tune the execution of goal-directed actions. This network facilitates the execution of context appropriate actions over competing actions by representing sensorimotor associations, likely based on rules specified by the pFPN (Bunge 2004; Koehlin et al. 2003; Petrides 2005). Thus, the SMN is involved in realizing proximal goals by specifying action patterns and their sensory consequences and contributes to an embodied sense of being an agent acting on the world.

7.6 Conclusions

In this chapter, we have outlined a simple deconstruction of goal-directed behavior based on the components operating over different time scales, from distal goals that span considerable periods of time to proximal goals that govern moment-to-moment interactions with the environment to the overt execution of specific actions. These components map onto three distinct brain networks that are organized along a roughly anterior-to-posterior axis in functional networks composed of frontal, parietal, and lateral temporal cortices. This cognitive and neural architecture underlying goal-directed behavior is consistent with the notion of a hierarchical organization, with neurocognitive components pertaining to longer time scales governing those pertaining to shorter time scales. The findings reviewed here offer a systems-level account of how we achieve personal goals and offer a window into the constituent elements making up complex human behavior. While we have sketched a view of the spatial topography and functional relevance of three brain networks relevant to goal-directed behavior, it is important to note that network properties change across time and context (Dixon et al. 2017). Thus, our review provides a “bird’s-eye view” of brain networks and goal-directed behavior; however, future work may reveal more precise cognitive and neural components.

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