Connecting and Networking

Proposed Brain Networks and Regions (Cerebral Topology & Hodology)

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CONNECTING: BRAIN NETWORKS AND REGIONS (CEREBRAL TOPOLOGY & HODOLOGY)

Topology & Hodology.

One of the fastest growing areas of neuroscience research these days involves efforts to figure out how the many parts of the brain are connected. Using the multiple types of neuroimaging and other exploratory research methods (explained in earlier classes) and the tools of network and graph theory (explained above), neuroscientists have begun to suggest how the brain is organized and connected both structurally and functionally. The very fancy title for these efforts can be labeled as cerebral topology and hodology. This section of the notes will give you a general overview of what has been accomplished so far.

The older and more traditional efforts of neuroscience were directed to learn where things were in the brain. This is known as cerebral **topology**. *Topology* is the scientific (or mathematical) study of **specific places**. The term is derived from the Greek word τοποσ (*topo*s) meaning "place." The adjective is "topological."

Over the last twenty to thirty years more and more research has studied how those different places in the brain are connected and how these connected places work together as active networks. There is a new term that labels these efforts: cerebral **hodology**. *Hodology* is the study of **pathways** and, in neuroscience more specifically, the **interconnection of cells** in the brain. The term is derived from the Greek word ὁδος (*hodos*) meaning "path." The adjective is "hodological." These terms (*hodology* & *hodological*) are SO new that in the summer of 2015 they had not yet appeared in the *Oxford English Dictionary*!

1. Types of Connectivity Networks

There are various ways we can talk about connectivity networks in the brain. Two approaches are to look at networks as (a) *structural* vs. *functional* or (b) *task negative* vs. *task positive*.

> **Structural**: "Structural connectivity describes anatomical connections linking a set of neural elements. At the scale of the human brain, these connections generally refer to white matter projections linking cortical and subcortical regions. Structural connectivity of this kind is thought to be relatively stable on shorter time scales (seconds to minutes) but may be subject to plastic experience dependent changes at longer time scales (hours to days). In human neuroimaging studies, structural brain connectivity is commonly measured as a set of undirected links, since the directionality of projections currently cannot be discerned" (Sporns, 2013, p. 248)

> **Functional**: "Functional connectivity is generally derived from time series observations, and describes patterns of statistical dependence among neural elements. Time series data may be derived with a variety of techniques, including electroencephalography (EEG), magnetoencephalography (MEG), and functional magnetic resonance imaging (fMRI)...Functional connectivity is highly time-

> dependent, often changing in a matter of tens or hundreds of milliseconds as functional connections are continually modulated by sensory stimuli and task context. Even when measured with techniques that operate with a slow sampling rate such as fMRI, functional connectivity may exhibit non-stationary fluctuations (Sporns, 2013, p. 248).

Forms of functional connectivity networks

"Task Negative" • Resting State • Intrinsic

There are differing names given to functional connectivity networks in the absence of external stimulation. These include "task negative," "resting state," and "intrinsic" connectivity networks.

"*Task Negative*" networks are described by Raichle as "brain areas frequently seen to decrease its activity during attention demanding tasks" (Raichle, 2015a, p. 1444). This term is used in contrast to "Task Positive" networks as described further below.

"*Resting State*" networks is a term with multiple meanings (Northoff, 2015, p. 1). These include the notion that "Roughly, the brain's resting state activity describes the brain's neural activity in the absence of any specific tasks or stimuli" (p. 1). Note, though, that a decrease in activity may not signal "resting" as much as "inhibition" so that the lack of activity in some conditions like major depressive disorder is an inhibitory phenomenon rather than a kind of idling or going into neutral.

"*Intrinsic" networks*: To avoid confusion suggested by the term "resting-state" networks, ICN is used to denote those "finite set of distributed spatial maps" [i.e., networks] that demonstrate "coherent brain activity…in the absence of an externally cued task" (Seeley, et al, 2007, p. 2349)

"Task Positive"

Task Positive networks = "commonly increase activity as a result of cognitive task engagement independent of the specific task…The general task activation pattern suggests an involvement of these regions in foundational capacities such as attentional control common to cognitive performance in general." (Sadaghiani et al, 2014)

- The task+ system is composed of at least three subgraphs (networks), corresponding to the fronto-parietal task control, cingulo-opercular task control, and dorsal attention systems. (Power et al, 2011, p. 671)

Because of the dynamic fluctuation across time as the brain deals with multiple task demands, active functional networks emerge for brief periods of time according to the task being performed. There is, as yet, no estimate or taxonomy of what those specific networks might be. As an alternative to the massive modularity hypothesis, there may be thousands of such functional networks with come in and out of use.

Task Activation Ensemble (TAE, Seeley et al., 2007)

“Regions such as the dorsal anterior cingulate cortex (dACC), orbital frontoinsula (FI), lateral prefrontal cortex (PFC), and lateral parietal cortex are consistently recruited by cognitively demanding tasks and frequently interpreted as constituting a unitary network, which we refer to as the task activation ensemble (TAE)” (Seeley, et al, 2007, p. 2349)

2. Is there a topological "Central" core?

Note: "In the context of biology, **homology** is the existence of shared ancestry between a pair of structures, or genes, in different species. A common example of homologous structures in evolutionary biology are the wings of bats and the arms of primates." {Wikipedia}

[In studying the most complete set of connection data of the macaque monkey brain] we ... discovered two remarkable bridges between the brain’s structure and function via network theoretical analysis. First, prefrontal cortex contains a disproportionate share of topologically central regions. Second, there exists a tightly integrated core circuit, spanning parts of premotor cortex, prefrontal cortex, temporal lobe, parietal lobe, thalamus, basal ganglia, cingulate cortex, insula, and visual cortex, that includes much of the task-positive and task-negative networks and might play a special role in higher cognition and consciousness" (Modha & Singh, 2010, p. 13485, [introductory comment added])

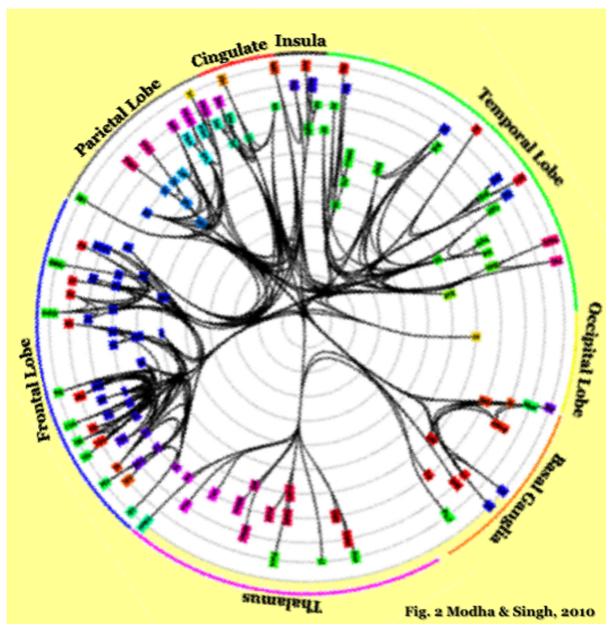


Fig. 2 Modha & Singh, 2010

“We have found a deeply nested and tightly integrated core circuit spanning the entire brain that contains both the task-positive and task-negative networks. ***Assuming homology***, it is indeed reassuring that the core circuit computed using structural data from a half century of anatomical tracing data in nonhuman primates corresponds so well with 3 decades of behavioral imaging research in humans. This hints at ***an evolutionarily preserved core circuit of the brain*** that may be a key to the age-old question of how the mind arises from the brain” (Modha & Singh, 2010, p. 13490, emphasis added)

“This work [Modha & Singh, 2010] described a tightly integrated “core circuit”, spanning parts of premotor cortex, temporal cortex, parietal cortex, prefrontal cortex, thalamus, “basal brain” (subcortical nuclei at the base of the forebrain, including the amygdala and basal ganglia), cingulate cortex, insula, and visual cortex. The core circuit was proposed to be “topologically central” – that is, strongly connected to all other regions of the core and the rest of the brain – and to have several important properties: (i) it is a sub-network that is far more tightly integrated than the overall network; (ii) information likely spreads more swiftly within the core than through the overall network; and (iii) the overall brain network communicates with itself mainly through the core.” (Pessoa, 2014, p. 404).

3. Individual Functional Networks

(A) Intrinsic & "Resting State" Networks

1. Default Mode Network (DMN)

Involved in internal tasks like daydreaming, self-reflection, and thinking about others. It is most active when a person is not focused on the outside world. (Claude.ai)

> “the default mode network is hypothesized to perform functions such as self-referential activities, future planning, self-inspection, and emotion regulation, the role of which diminishes during traditional cognitive tasks” (Sylvester et al, 2012, p. 531)

The DMN shows greater activity during resting state ("task negative") conditions compared to performing cognitive tasks.

Location. Raichle (2015a) proposes that the DMN is comprised of three major subdivisions:

- ventral medial prefrontal cortex (vMPFC)
- dorsal medial prefrontal cortex (dMPFC)
- posterior cingulate cortex (PCC) & adjacent precuneus plus the lateral parietal cortex (approximately Brodmann area 39).
- The entorhinal cortex or the parahippocampal gyrus of the temporal lobe) has also been frequently associated with the DMN.

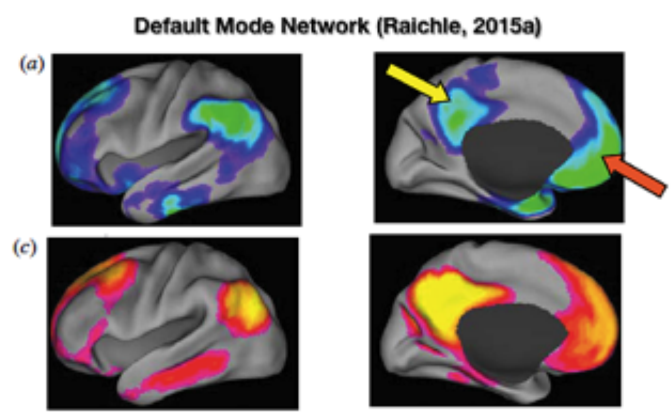


Fig. 2. (a) decreased activity during task performance; (c) resting-state functional connectivity

Functions. Various theories have been proposed for the functions of the DMN. In reverse chronological order these include the following:

Buckner & DiNicola (2019) indicate that “detailed high-resolution analyses of single individuals suggest that the default network is not a single network , as historically described, but instead comprises multiple interwoven networks.” (Abstract)

- In the DMN differential activation of “distinct juxtaposed regions” is seen in neuroimaging "when tasks involving remembering are contrasted with tasks requiring inferences about other people's thoughts and beliefs (theory of mind). Tasks that tap into autobiographical memory preferentially engage the parahippocampal cortex and the ventral portion of the posterior midline, near to the retrosplenial cortex. Within the inferior parietal lobule, tasks involving remembering also engage more- posterior (that is, caudal) regions, whereas theory-of-mind tasks preferentially engage more-anterior (that is, rostral) regions extending into the temporoparietal junction" (p. 4)

- "Evidence emerging from … studies suggests that the default network comprises at least two separate networks with clear spatial distinctions along the posterior and anterior midline, which have often been described as hubs of convergence."(p. 5)
- "A clue to the origins of specialization in the two principal networks linked to the default network (termed default network DN-A and DN-B) is that DN-A is strongly coupled to posterior parahippocampal memory structures, whereas DN-B is not" (p. 6)
- In this scheme, DN-A may be related to episodic and autobiographical memory functions while DN-B may be related to mentalizing social tasks such as trying to understand what another individual is thinking (theory-of-mind tasks) (See Braga & Buckner, 2017)

Raichle (2015a) offers multiple comments about functioning in the DMN. These include

- vMPFC - processes that support emotional processing
- dMPFC - self-referential mental activity
- Posterior elements - recollection of prior experiences
- DMN ≠ spontaneous cognition alone, i.e., "unconstrained, conscious cognition [i.e., mind wandering or daydreaming"]
- "Begins with baseline of high activity…never turned off…carefully enhanced or attenuated"
- Plays " a critical role in the organization and expression of preplanned, reflexive behaviors that are critical to our existence in a complex world but when unconstrained by the social and physical constraints of the environment become impulsive and destructive."

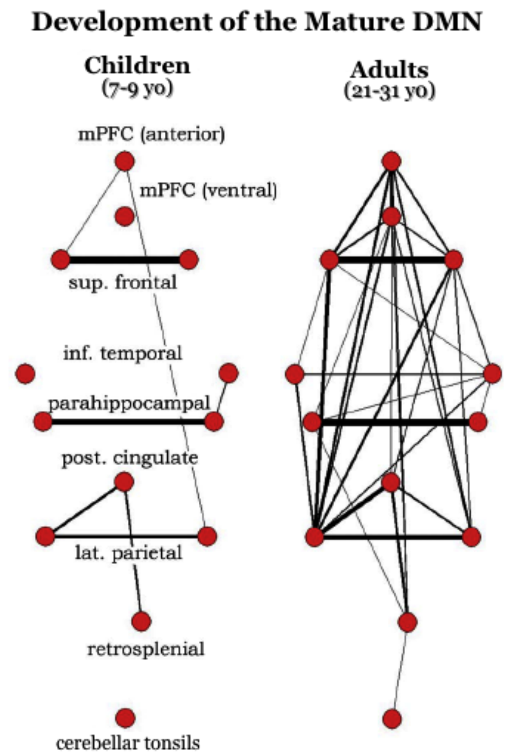
Nielsen et al. (2013) propose that there are two major subsystems in the DMN

- Considering one's own present mental state (Subsys 1/dMPFC)
- Episodic decision making about the future, i.e., recalling the past and thinking ahead (Subsys 2/MTL)
- Both subsystems are active when the person is involved in spontaneous thinking such as "daydreaming."

Fair et al. (2008) examined DMN development in children vs. adults and emphasize the adult DMN as involved in

- ‘‘self-referential’’ or ‘‘introspective’’ mental activity, and
- ’’internal narrative,’’ the ‘‘autobiographical self,’’ ‘‘stimulus independent thought,’’ ‘‘mentalizing,’’ and “self-projection’’ particularly in respect to the medial prefrontal cortex.

However, they also found clear evidence that "the default regions are only sparsely functionally connected at early school age (7–9 years old); over development, these regions integrate into a cohesive, interconnected network" (p. 4028).



Fair et al (2008), Fig. 3

History. In 2001, Marcus Raichle and his colleagues first identified what they called “a default mode of brain function.” This new understanding of the brain came when Raichle (and other researchers) began to notice the difference in the patterns of blood oxygen use via fMRI images between brains that were (1) actively doing something versus (2) quietly “resting” (i.e., during the periods in-between activities). Certain areas during these resting periods steadily used a certain amount of oxygen (indicating, therefore, that the neurons were doing something) and, when individuals were given a particular task, these resting areas became deactivated (they decreased their oxygen use). Thus, there seemed to be a default mode of activity in the brain when it was not actively working on a task.

2. Executive Control Network (ECN)

[aka Central Executive Network (CEN) or Fronto-parietal Control Network (FPCN)]

Involved in cognitive control and flexibility. It helps adjust control based on feedback (Claude.ai).

Location (Seeley, 2007, p. 2352)

- **bilateral dorsal lateral prefrontal cortex** (DLPFC)
- **bilateral ventrolatral prefrontal cortex** (VLPFC)
- **dorsomedial prefrontal cortex** (DMPFC)
- **lateral parietal cortex** (LPC)
- a site in the **left frontoinsula**
- **dorsal caudate** & **anterior thalamus**

Functions (Seeley et al., 2007)

"[**O**]**perate**[**s**] **on identified salience**. Such operations require **directing attention to pertinent stimuli as behavioral choices are weighed against shifting conditions, background homeostatic demands, and context.** To achieve this level of response flexibility, the brain must exert control over posterior sensorimotor representations and maintain relevant data in mind until actions are selected. A network geared for this purpose should, and appears to include known sites for **sustained attention** and **working memory** (DLPFC, lateral parietal cortex), **response selection** (dorsomedial frontal/ pre-SMA), and **response sup-pression** (ventrolateral prefrontal cortex)" (Seeley, et al, 2007)

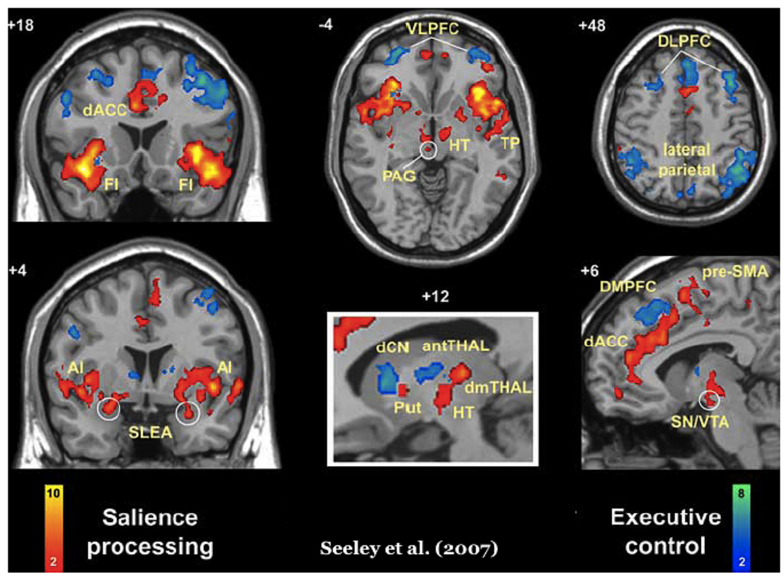


Figure 2. ***Salience Network*** (red-orange colorbar) is anchored by paralimbic anterior cingulate and frontoinsular cortices with extensive connectivity with subcortical & limbic structure. ***Exective-Control Network*** (blue-green colorbar) includes the dorsolateral frontal & parietal cortices linked with more selective subcortical coupling.

AI Anterior insula; antTHAL anterior thalamus; dCN dorsal caudate nucleus, dmTHAL dorsomedial thalamus; DEMPFC dorsomedial prefrontal cortex; HT hypothalamus; PAG periaqueductal gray; Put putamen; SLEA sublenticular extended amygdala; SN/VTA substantia nigra/ventral tegemental area; TP temporal pole; VLPFC ventrolateral prefrontal cortex . Also, dACC dorsal anterior cingulate cortex; FI orbitofrontal insula; preSMA presupplementary motor area

- "The FP network is proposed to support phasic aspects of attentional control such as exogenously triggered initiation of control, adapting after errors (Dosenbach et al. 2006) and moment-to-moment adjustment of control as in repeated rapid task switching (Seeley et al. 2007). These functions are well matched with the afore-mentioned notion of phasic alertness (Sadaghiani et al. 2012)" (Sadaghiani et al., 2014)

- Supports the "external focus of attention during goal-directed, cognitively demanding tasks" (Barbey et al., 2015, p. 94).
- **Dysfunctions to the ECN "results in the classic dysexecutive syndrome marked by impairments in externally oriented tasks that engage, for example, general intelligence, fluid intelligence, cognitive flexibility, working memory, and problem solving"** (Barbey et al., 2015, p. 95)
- Damage may lead to impaired self-awareness (Ham et al, 2014)

3. Dorsal Attention Network (DAN)

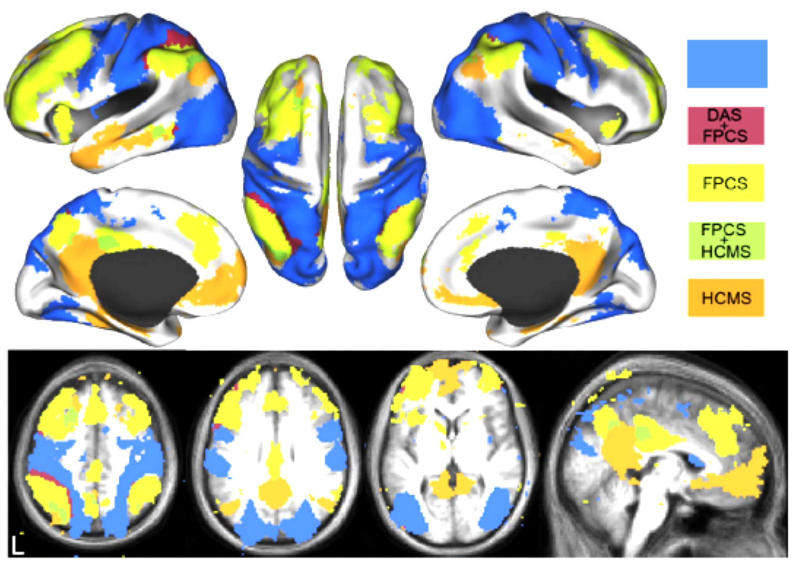


Fig. 7. Intrinsically defined dorsal attention (DAS), frontoparietal control (FPCS), and hippocampal-cortical memory (HCMS) systems and the overlap between them from dataset 3. Voxels in the DAS are shown in blue. Voxels in the FPCS are shown in light green. Voxels in the HCMS are shown in orange. Voxels significantly correlated with the DAS & FPCS are shown in red. Those correlated with the HCMS & FPCS are shown in dark green. Data are displayed on the lateral, medial, and dorsal surfaces of the left and right hemispheres as well as MNI atlas space axial and saggital slices.

Vincent et al (2008)

Involved in voluntary, goal-directed tasks that require external attention like working memory and cognitive control. It activates when attention is focused externally. (Claude.ai)

Location (Vincent et al., 2008)

- **frontal eye fields**
- **ventral premotor cortex**
- **superior parietal lobule**
- **intraparietal sulcus**
- **motion-sensitive middle temporal area** (MT+)

Functions

- The DAN "plays an important role in selecting visual information based on internal expectations or the sensory salience of visual objects." (Corbetta Lab @ Washington U.)

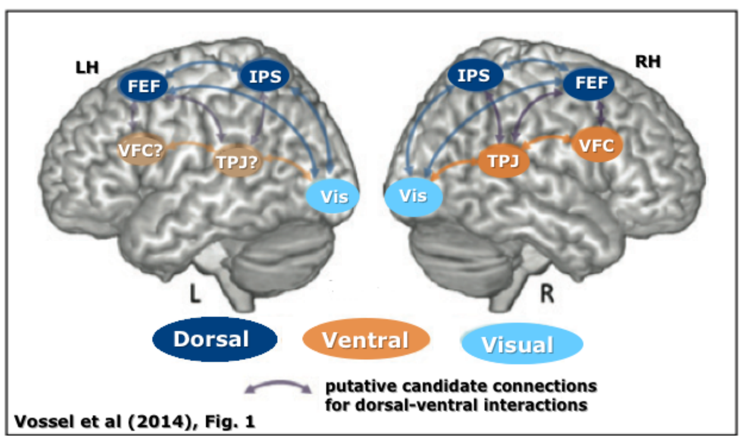
- Externally directed cognition including covert and overt shifts of spatial attention, eye movements, and hand-eye coordination" (Vincent et al, 2008).
- "The dorsal attention system selects information from the sensorium under the direction of top-down influences to enable the performance of externally oriented tasks, e.g., eye-hand coordination" (Vincent et al., 2008)
- "DAT network is proposed to underlie selective attention especially in visual and spatial domains (Corbetta and Shulman 2002; Fox et al. 2006). Selective attention enhances processing of specific sensory input over other input (Driver 2001) in all likelihood by increasing activity gain of the neural populations encoding the attended stimulus or feature (Chawla et al. 1999; Kastner and Ungerleider 2000)." (Sadaghiani et al., 2014)
- "detector of novel environmental features" (Raichle, 2015a)

4. Ventral Attention Network (VAN)

Involved in detecting salient stimuli in the environment and reorienting attention based on sensory input. It helps shift attention. (Claude.ai)

Location

- "is largely right-lateralized and includes the ventrolateral PFC (VLPFC), the temporal–parietal junction (TPJ), and portions of the middle and superior temporal gyri" (Sylvester et al., 2012, p. 530)



FEF Frontal Eye Field; IPS Intraparietal Sulcus; TPJ Temporal-parietal junction; VFC Ventromedial prefrontal cortex; VIS Visual cortex
? Suggested additional areas

- "The ventral attention network includes parts of the **ventrolateral PFC** and the **temporal–parietal junction** and is involved in directing attention to newly appearing stimuli. Increased functioning of the ventral attention network may be linked to increased attention to stimuli that suddenly appear rather than towards stimuli that are currently the focus of the task at hand" (Sylvester et al., 2012, p. 527)

Functions

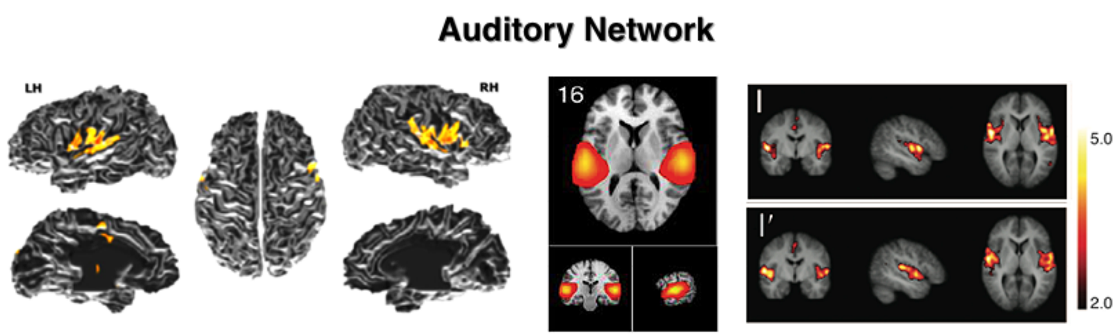
- "typically responds when behaviorally relevant stimuli occur unexpectedly (e.g., when they appear outside the cued focus of spatial attention)" (Vossel et al., 2014, p. 151)

- Stimulus-driven attention (Sylvester et al, 2012, Table 1)
- "is associated with the orientation of stimulus-driven attention – the automatic orienting to a particular location when a stimulus appears at that location" (Sylvester et al, 2012, p. 530)

"Although both dorsal and ventral attention systems are specialized for distinct attentional subprocesses such as top-down controlled attentional selection and the detection of unexpected but behaviorally relevant stimuli, respectively, it becomes obvious that flexible attentional control can only be implemented by dynamic interactions of both systems. Recent research has shown that this interaction pattern is flexible and crucially depends on the current task demands. Hence, activity in both systems can either be correlated or anticorrelated. There is evidence that this interplay is governed by frontal areas such as the inferior and middle frontal gyrus. The hemispheric functional specialization of each system and of their interaction needs to be addressed by future studies" (Vossel et al, 2014, p. 157)

B. Sensorimotor Networks

1. Auditory Network (AUDN)



Adapted from Ganzetti & Martini (2013)   Laird et al (2001), Fig. 2   Damoiseaux et al (2006), Fig. 1

Involved in processing auditory information even at rest. It covers auditory cortices. (Claude.ai)

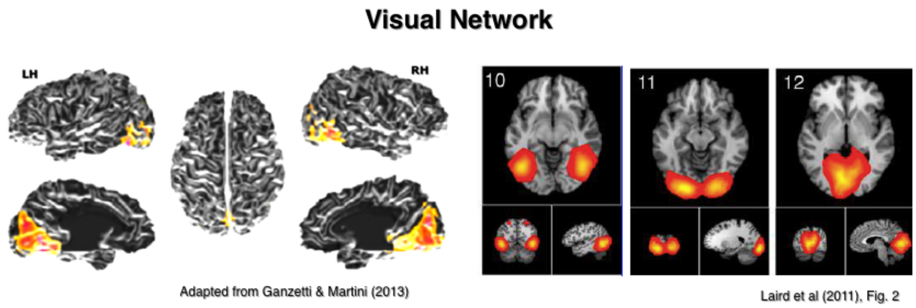
Location

- Superior temporal cortex
- BA1 & 2 (insula & postcentral cortex)

Function

- Tone, pitch discrimination
- Speech, music

2. Visual Network (VISN)



Involved in processing visual information even at rest. It covers the visual cortices. (Claude.ai)

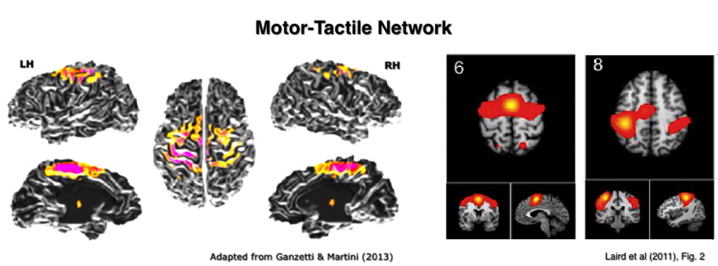
Location

- Lateral and medial posterior occipital cortices) included the primary, secondary, and tertiary visual cortices (V1, V2, V3; BA 17/18/19; #11-12 in fig. above)
- Middle and inferior temporal gyri included the middle temporal visual association area (MT, MST, V5; BA 37/39) at the temporo-occipital junction (#10 in fig. above.)

Function

- "Simple visual stimuli [#12 in fig above]… higher level visual processing associated with orthography [handwriting] and covert [silent] reading…Braille reading, demonstrating observed plasticity of these cortical regions in blind subjects [#11 in fig. above]" (Laird et al. 2011, p. 4030)
- "Viewing complex, often emotional, stimuli (e.g., faces, films), as well as action observation, overt picture naming, and visual tracking of moving objects, particularly random dot formations. Other tasks included mental rotation and the discrimination of locations in space" (#10 in fig. above; Laird et al., 2011, p. 4030)

3. Motor-Tactile Network (MTN) (aka Sensory-Motor Network)



Involved in sensory-motor processing. It covers sensorimotor cortices. (Claude.ai)

Location

- Superior & middle frontal gyri (Laird et al., 2011): premotor & supplementary motor cortices (BA6) & frontal eye fields (BA 8 & 9; #6 in fig above right)
- Ventral pre-central gyri, central sulci, postcentral gyri, superior & inferior cerebellum (BA 1, 2, 3, 4; #8 in fig. above right).

Function

- cognitive control of visuomotor timing and preparation of executed movements (Laird et al., 2011, p. 4029)
- action & somesthesis (= "All of the various sensory systems in the skin and other bodily tissues responsible for the senses of touch-pressure, warmth and coldness, pain, itch together with positioning and movement"-*Wiktionary*) corresponding to hand movements, includes tasks such as finger tapping, grasping, pointing, electrical and vibrotactile stimulation & TMS" (Laird et al, 2011, 4029)

C. Other Functional

1. Salience Network (SALN)

Involved in detecting and filtering relevant internal and extrapersonal stimuli to guide behavior. It helps determine what is most relevant to pay attention to. (Claude.ai)

Location

- Anterior cingulate cortex (ACC)
- Presupplementary motor areas (preSMA)
- Anterior insula (AI)

Function

- Signals the need for behavioral change" (Bonnelle et al., 2012, p. 4690)
- "Integrate[s] highly processed sensory data with visceral, autonomic, and hedonic [reward-giving] "markers," so that the organism can decide what to do (or not to do) next." (Seeley et al, 2007)
- The nervous system is continuously bombarded by internal and extra-personal stimuli. A leading priority is to identify the most homeostatically

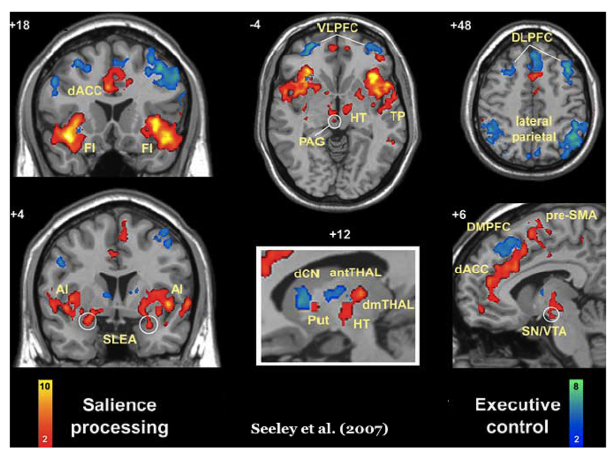


Figure 2. ***Salience Network*** (red-orange colorbar) is anchored by paralimbic anterior cingulate and frontoinsular cortices with extensive connectivity with subcortical & limbic structure. ***Exective-Control Network*** (blue-green colorbar) includes the dorsolateral frontal & parietal cortices linked with more selective subcortical coupling.

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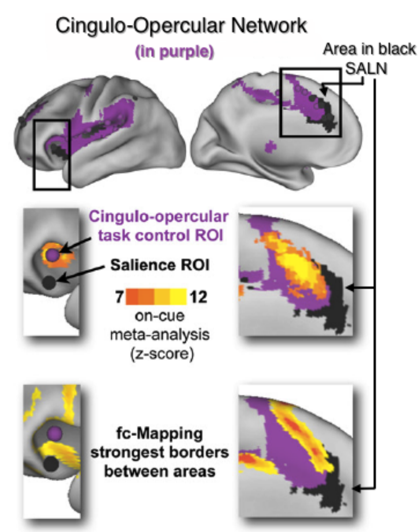
- "An object or event is ***salient*** if it is significant to an individual. The signals can come from inside the body, such as pain or hunger, or outside, such as the sound of a distant siren while driving in traffic…The more salient something is, the more it captures our drive system, which directs behavior." (Singer, 2013, para. 4 & 5)
- "At least part of the salience network's role seems to be linked to something very basic: the fight or flight response. That response — an accelerated heart rate, dilated pupils and rising blood pressure, readying the body for action — may be orchestrated by the salience network" (Singer, 2013)
- "Too much activity in the salience network can also be problematic. Seeley and Greicius's original [2007] study found that the people who reported the most anxiety before they entered the brain scanner also showed the strongest network connections" (Singer, 2013)
- The SALN is closely coordinated in normal individuals with the DMN. However, in the presence of TBI which affects the SALN, the Default Mode Network may not deactivate and the individual may not be able to respond to environmental cues (Bonnelle et al, 2012, summarizing p. 4693)

2. Cingulo-Opercular Network (CON)

After the initial identification of the SALN network (Seeley et al, 2007), later research suggests that it may be part of a larger network termed the *Cingulo-Opercular Network* (CON) involving a "domain-general" role to promote *cognitive control*. Sadagihiani & Esposito (2014) argue that there are two subdivisions to the CON: a partial CON (CO^P) and the SALN described above. The characteristics of the CON, particularly the CO^P are described below.



Adapted from Power et al (2011), Fig. 4

Location

- Anterior insula/operculum (bilateral)
- Dorsal anterior cingulate cortex (bilateral)
- Dorsal anterior prefrontal cortex (bilateral)
- Thalamus
- Right anterior inferior parietal lobe

Function

"The sustained involvement of the CON over the extended course of a trial adds support to the idea that the network is involved **in maintaining a task set** (Dosenbach et al., 2006), **coordinating or sequencing task processes**, or **maintaining sustained effort** (Sterzer & Kleinschmidt, 2010), perhaps coupled with transient processes related to error and salience detection" (Sesteiri et al, 2014, p. 12, emphasis added).

Tonic Alertness: "**a sustained and endogenously maintained type of top-down control process** distinct from attentional control processes that are phasic in nature. This sustained function is referred to as "vigilance" (Mackworth 1948; Parasuraman 1998), "vigilant attention" (Robertson and Garavan 2004), "sustained attention" (Warm 1984), or "tonic alertness" (Posner 2008). In these accounts, this sustained function—henceforth called tonic alertness—is described as the mentally effortful, self-initiated (rather than externally driven) preparedness to process and to respond." (Sadaghiani et al, 2014, emphasis added)

"The concept of alertness extends beyond situations in which a known task-set is maintained and includes alert states of high vigilance in which information about the environment, the potential sensory input and the need for action is lacking or sparse (such as in a dark unfamiliar environment with potential threats). While task-set maintenance involves the maintenance of specific information about the task, tonic alertness emphasizes the general mechanism of keeping cognitive faculties available for current processing demands and holding unwanted activity at bay" (Sadaghiani et al, 2014).