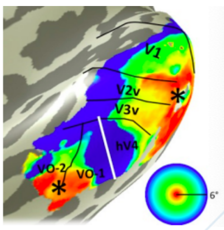
MAPS, GRADIENTS, HIERARCHIES

Generality

Internal organisation of the brain:

- Map=one-to-one correspondence of a portion of the brain to a specific area of the body (somatotopic mapping) or to a part of the external world (ex retinotopic mapping based on eccentricity)
- Hierarchy=the direction of elaboration in brain areas goes always from a higher grade to lower order regions→ from a concrete representation to an abstract one, also a control hierarchy (ex top-down)
- Gradient=vector along which cortical features continue changing in a spatially continuous order
    - somatotopic map=point-to-point body-brain correspondence
        - ex sensory/motor regions→ Penfield's homunculus
    - retinotopic maps=ordered maps of the visual space, inverse directions from reality, magnification pattern: fovea is over-represented, bc of higher presence of cones, vs more rods in the periphery=higher convergence)
        - eccentricity maps

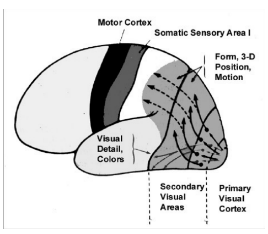


- in the visual cortex, at the centre fovea, then the rest of the retina is more lateral
- → these differences are already present at birth. Inside the maps, areas are represented as overlapping gradients rather than as precise and confined regions

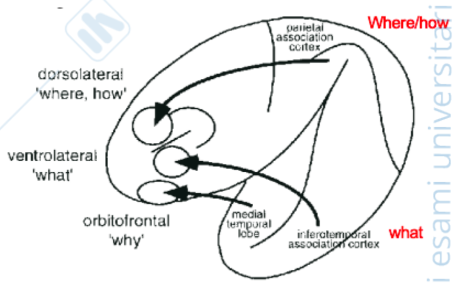
Visual streams

The two visual streams are an example of brain hierarchies=pathways which lead to a progressively more complex representation of stimuli

- Hierarchical=each stage comes from the previous one, through feedback connectivity higher level regions control lower ones→ visual elaboration is progressive
- Possible through U-shaped short association fibres of white matter, from neighbouring gyri to form the visual streams→ the info travels from simplest elaboration to the most advanced/complex visual and semantic representation
    - integrated from primary to secondary and associative regions
    - from an associational pov, we expect associations that permit this organisation
        - short association fibres in dorsal and ventral stream

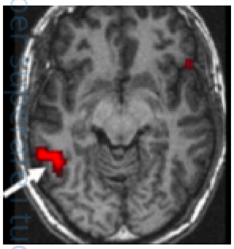


    - tractography in vivo (Catani): U-shaped fibres in inferior occipito-temporal cortex to inferior longitudinal fasciculus
- The pathways originate from the distinction between magnocellular (M) and parvocellular (P) pathways in the LGN of the thalamus
    - M code for movements, trajectories and depth (transient activation)
    - P code for colours and contrast (stabile activation), respectively info from rods and cones in the retina
- From occipital areas, move anteriorly

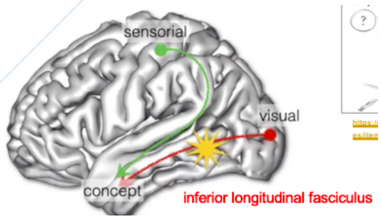


There are two pathways

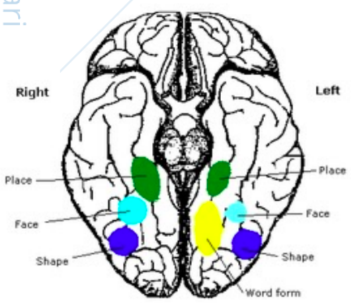
- Ventral visual stream="what" pathway=progressive coding for the identity of visual objects, first divided in their smallest component (colour, frequency, etc) and then perceived as a whole
    - from occipital to temporal lobe
    - pure Alexia=acquired reading deficit in previously literate people
        - see neurosurgery case study (Epelbaum): resection of an epileptic focus
        - disconnection syndrome: deafferentation between VWFA and other language regions
        - visual word form area fMRI activation (words-checkerboards)



    - achromatopsia=blindness to colours
        - cause: damage in V4 or disconnection from visual input (codes for colour), can be unilateral (hemi-acromatopsia, madame R) or bilateral (bilateral full-field, madame D)
        - can be a disconnection syndrome

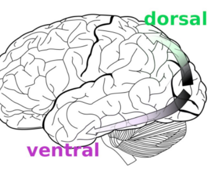


    - visual agnosia=the patient cannot name an object if presented through vision (but can through touch)
        - disconnection between visual areas and semantics/conceptual areas (inferior longitudinal fasciculus damaged)
        - ≠ amnesia
    - acquired prosopagnosia (Bodamer)=inability to recognize the identity of familiar faces after a lesion/brain damage
        - possible in isolation with intact visual perception and ability to recognize non-face objects) → familiar people are recognizable from other sensory cues (ex voice)



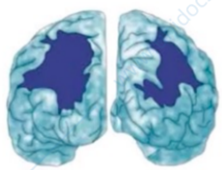
        - cause: bilateral or right damage in the medial occipito-temporal cortex (preference for face recognition), especially in the FFA, which forms a network with the PPA and LOC (identity of non-face objects, codes for shapes)
            - from a localizationist pov, the FFA is responsible for face recognition (ventral stream) → parahippocampal space area
            - N170: ERP negativity occurring at 170 ms after face onset (face perception marker)
                - Bentin: recognising inverted face is associated to an increase of N170 latency

        - more dominant in the RH, for inverted faces longer latency and less amplitude
    - its neural sources were initially unclear (Bentin) → among suggestions, could involve the FFA but also other components in the face processing system, such as the occipital face area (OFA) and STS (superior temporal sulcus)
    - to have a better understanding, neuropsychological studies in patients with selective lesions in the areas of the face recognition network: ERP recordings showed that if the lesion wasn't in the face recognition network, N170 preserved
        - some had lesions in occipital face area, or FFA or With a lesioned FFA, preserved N170
        - ant intact FFA is not sufficient to produce N170
    - with a lesion encompassing both OFA and FFA, no N170 was recorded→ at least two nodes of the network have to be damaged to affect the N170
    - limitations:
        - limited cohort of patients
        - no patients with STS damage
        - OFA damage was never observed in isolation = no possibility of isolating its role from the FFA
    - → an intact FFA is not enough to produce the N170 (against localizationist models)
    - Cohen: lesion network mapping=regions consistently damaged in patients with prosopagnosia were superimposed on a map based on healthy brains to visualise how such lesions would affect the networks in which they are included
        - FFA is always impaired, especially bc of connectivity damage→ if the FFA was not lesioned, at least was disconnected with the other lesion area
        - all lesions were negatively correlated to the lPFC→ prosopagnosia comes from lesions in a network which includes the right FFA and left PFC
        - for all lesions causing prosopagnosia, lesion locations demonstrated positive (right fusiform gyrus) and negative (left frontal cortex) correlation to a specific set of locations



- Dorsal visual stream="where/how" pathway=encodes spatial info=size, location, movement, geometrical organisation→ from occipital to parietal regions
    - simultanagnosia (Wolper)=inability to perceive more than a single object at the same time/deficit in integrating different objects to form a single story/scene and in understanding the overall meaning of it

            - evaluation
                - task where you have to unify stories from images
                - Navon task=focus on the global shape or the local letters (compatible vs incompatible)
                    - NB! Multiple objects may be covertly elaborated: in the Navon task facilitation in colour naming if the big letter is the initial of the colour of the small letters
            - bilateral parieto-occipital lesions
        - optic ataxia=inability to move the hand to a specific target object presented in the visual modality with a manual mis-reaching (especially peripheral)
            - no problem in seeing and describing the orientation
            - bilateral lesions at the posterior parietal cortex, but also disruption of connectivity in the dorsal or between dorsal and premotor in frontal lobe



        - Balint Syndrome=symptoms from simultanagnosia, optic ataxia and oculomotor apraxia
            - bilateral lesion to posterior parietal regions (especially to the angular gyrus)

Oculomotory apraxia=inability to voluntarily perform purposeful eye movements, ex following a moving object

        - akinetopsia=inability to perceive movements/moving objects→ failure to integrate sequential fixations in fluid images
            - rare: due to localised lesion in the medio-posterior temporal cortex (V5/MT)

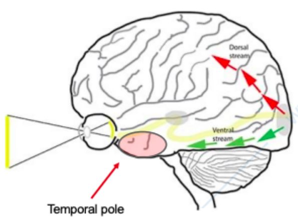
Dissociations between ventral and dorsal visual streams (Goodale & Milner, 1992):

- blindsight=patients with visual field defects (anopsia=damage in V1) claim they don't see anything in their visual field, but actually have got residual visual abilities for stimuli placed in their blind fields→ if forced to do, they can detect where stimuli are but can not see them
    - processes of recognition can be damaged separately from those for interaction
        - some pathways for visual info don't rely on V1 (ex subcortical)
    - different types of blindsight
        - colour
        - orientation
        - action=using a pointing paradigm, a patient with left hemianopia showed clear above chance manual localization of 'unseen' targets, consciously thinks they're acting randomly
    - the patient can act on the object without actually seeing it

Other areas

Temporal pole=amodal hub for semantic processing→ semantic hubs are also present in other areas, but less consistently

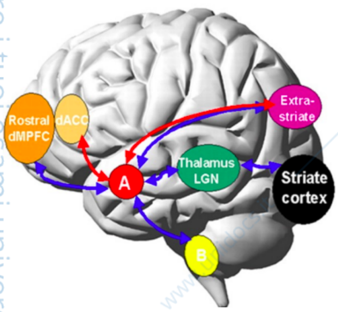
- end of the ventral stream
- semantic dementia is caused by cortical atrophy in the anterior temporal lobe=damage to the semantics system (no meaning of words)



    - different from Alzheimer's disease: cortical thinning in other regions, more related to memory
- there can be other semantic deficits, since different pathways (visual, tactile, auditory) access the semantic system in the TL
        - if auditory connections are lost and the connection with the semantic hub is interrupted, the auditory order is understood but the patient repeats in a loop what he's asked to do, must access the concept through the connection between the semantic hub and the verbal processing area to repeat it
            - alternative route, through Broca and premotor area=repeat herself, then back to the meaning to execute
            - if the sentence is too complex, the patient may fail

Connectivity between visual and limbic system

- The visual area is connected to the amygdala, especially for emotional visual inputs
    - lesion to the amygdala, the visual
- Important connections to the amygdala=emotion
    - connected to the visual area, especially if we're seeing emotional inputs
    - lesion to the bilateral amygdala, the visual cortex cannot get inputs from it for emotional representation
    - case study: patient with bilateral destruction of the amygdala caused by Urbach-Wiethe disease (rare recessive genetic disease, calcification of the amygdala) → incapable of recognizing fearful faces, while other emotions can be understood
        - dissociation in recognition of fear and of faces→ the amygdala is required to link the representation of facial expressions and of fear
        - task of drawing a fearful face: figure with some stereotypical features of fear (ex shaking) but without frontal view→ visual representation and concept of fear
        - the amygdala is involved in processing emotion, but specifically fear



Is the subdivision of the streams maintained in frontal regions?

- Working memory model in monkeys (Goldman-Rakic): labelled line model, there's a distinction in the working memory in the PFC for spatial elements and objects
    - what: object working memory (inferior ventral-lateral PFC)
    - where: spatial working memory (dorsal caudal sulcus principalis)
        - dorsal visual stream
    - motivational aspects: OFC→ codes for rewards in goal directed behaviour
    - → working memory may depend on inputs from the visual streams, with the degree of specialisation depending on connections
- In humans, controversial data with fMRI:
    - pro: Courtney

- task: remember the location vs the identity of faces, then memory test: position? vs presented before?
- results: for spatial WM dorsal activation, for object WM ventral activation
- areas with significant sustained activity in a single individual during the working memory delay for faces and for spatial locations

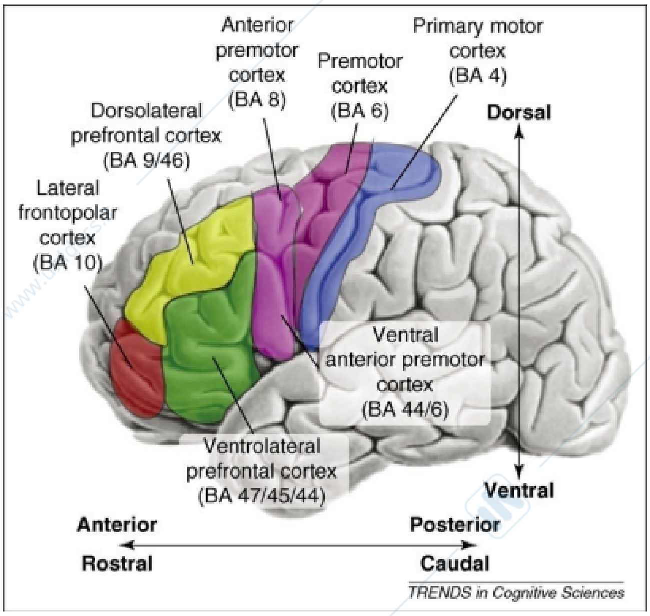
- contra: D'Esposito
  - initial review of the literature: the differential activation in the left PFC (dorsal vs ventral) seems to be linked to a difference in maintenance only tasks vs manipulation tasks (actual WM)
  - fMRI study: tasks with spatial vs non-spatial WM, no differential activation, all evidence points to a distinction between storage (vlPFC) vs manipulation/monitoring (dlPFC)
- In subsequent studies, working memory processes have been localised to the vlPFC for short-term memory storage and to the dlPFC for manipulation/monitoring in WM
  - Petrides: old/new task vs maintenance to never select the same one, paintings, select one and touch it: some of the pairs would come back again and if so, they would need to select the stimulus they didn't touch (monitoring/remembering component)
    - short term memory storage: ventrolateral PFC
    - manipulation/monitoring in working memory: dorsolateral PFC

Caudo-rostral prefrontal hierarchies/gradients=from motor cortex, to more anterior prefrontal regions

- Temporal organisation of behaviour (Fuster): PFC=executive functions=mediation of cross-temporal contingencies between events, words, stimuli, acts
  - temporally prospective (if now X, then later a specific action) vs retrospective (if earlier X, then now a specific action)
  - hierarchical organisation of functions (executive+perceptual cognits), parallel to the passage of info in different areas
    - from very concrete to abstract representation // from sensory cortex to associative and prefrontal cortex, through associative regions (parietal)
    - advanced dorsolateral prefrontal regions (dlPFC)=top of sensory-motor hierarchies, integrate/guide perception-action cycles thanks to a close cooperation with structures lower in the hierarchy
    - NB! Coexistence of
      - topographic specificity within PFC=some regions respond more to some types
      - overarching role=bridging temporal gaps & organising new actions in all domains (behaviour, reasoning, language)
  - model tested on monkeys with delay-task paradigms
    - tasks: delayed response vs delayed matching to sample (where the stimulus appears)
      - results: cooling the dlPFC produced reversible deficits in visual, auditory and tactile delay tasks

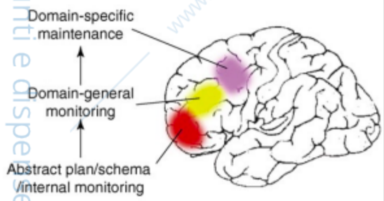
        - single-unit recording study, delayed matching of a tone to a colour: most recorded units in the PFC keep the firing rate for the specific tone until the choice of the colour
            - keep representing the correct stimulus to later guide behaviour
    - as you move away from concrete representation, you can take a temporally prospective or retrospective
- Miller's model: PFC shows computational capacities as it permits inductive reasoning=extracts empirical info about the regularities across experiences to impart rules→used to guide thought and action
    - abstract knowledge→ generalisation
    - evidence
        - most lateral PFC neurons reflect the association between a cue and reward: integration of actions/stimuli with their consequences
        - the activity of 44% of lateral PFC neurons reflects associations between objects and the action they instruct
        - PFC neurons can reflect learned associations between visual and auditory stimuli (Fuster) → integration of actions and reward
- Badre identifies organising principles along the rostral-caudal (Y) axis:
    - posterior regions: control of temporally proximate, concrete action representations
    - anterior regions: control of temporally extended, abstract representations
    - → depending on the type of task, the same prefrontal regions change their connectivity with more posterior regions

10–10

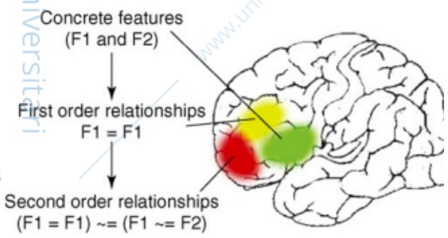


Models

- Model do not agree on the meaning of abstraction and on the processes underlying the interaction between levels
    - even if a task can be represented hierarchically, this does not guarantee that the action system itself consists of structurally distinct processing levels
        - hierarchical=top-down influence too, non-hierarchical=just sequential processing
    - Botvinick & Plaut (2004) demonstrated that goals and subgoal representations of sequential actions can be represented simultaneously in a single layer neural network
        - need of neural evidence to establish whether anatomically distinct neural processors support hierarchical representation and control of action
- Models classified into 2 groups:
    - domain generality in WM: content-based distinctions reported in posterior prefrontal regions but domain-independent representations in rostral prefrontal regions



        - hierarchical organisation=activation during the preparatory interval in anterior DLPFC/frontopolar cortex correlates with activation in SFG (BA 8) or IFG (BA 44) depending on whether the prepared task is spatial or verbal, respectively
            - abstraction=domain-generality
    - relational complexity in PFC=different levels of relational complexity along the Y-axis
        - Concrete features: maintains rules involving item properties (ex What is the colour?)
            - ventrolateral PFC
        - First-order: maintains simple relationships between concrete properties (ex Do the colours match?)
            - dorsolateral PFC
        - Second-order: evaluates relationships among relationships (ex "does the mismatching dimension of a target pair match the mismatching dimension of another pair?")
            - fronto-polar cortex
            - → here: abstraction = relational complexity
            - the **fronto-polar cortex** integrates the outcomes of multiple cognitive operations, including relational ones, in the pursuit of a higher behavioural goal
                - NB! Here higher-order relationships depend on lower-order ones but not vice versa→ not strictly hierarchical: no asymmetrical feedback from higher to lower levels
            - "superexperts" can keep in mind motor plans: they do not keep engaging higher level cognitive control functions, they learn how to use a repertoire of stored representation and they're efficient and quick
                - while learning you use parietal/associative regions, when you've learned, it becomes automatised and the regions become autonomous

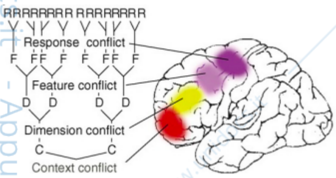


Cascade model (Koechlin&Summerfield)=hierarchy driven by control signals

- PFC applies control on other regions, resolving competition among alternative action representations (lower level) based on control signals from a number of sources
  - control=reduction of uncertainty among the possible responses given extra signals (sensory, contextual,...) → control signals are hierarchically related=top-down
- The different levels of control can be characterised by the kind of control signal, the output and their location:
  - sensory control: from sensory input (stimulus) to motor response (PM cortex)
    - most basic→ automatic movement
    - the phone rings, I answer
  - contextual control: environmental contextual clue to action,
    - posterior PFC
    - the phone rings, but it's not mine, instead of answering, I warn my friend
  - episodic control: ongoing temporal context → action
    - anterior dlPFC→ inhibit M1 that was inhibiting the movement to answer
    - my friend asks to answer their phone while he's in the bathroom: if it starts ringing, movement to answer
  - branching control: pending (=could be resumed) temporal context to action representation
    - fronto-polar cortex
    - branching = highest level of control, basis of all behaviour requiring simultaneous engagement in multiple tasks
    - the friend comes back from the bathroom but says that he's going to leave again in some time: don't answer the phone if it rings, but keep the representation to resume the task later
- Empirical evidence (Koechlin): fMRI study with 4 different tasks: uppercase or lowercase, taken from "tablet"
  - I. Control task: two capital letters are presented in sequence, are they subsequent in the word tablet?
  - II. Delayed task: same task as the control condition, but between capital letters there are lowercase ones to distract and delay the response
  - III. Dual-task: capital and lowercase letters are presented mixed together: when changing from capital to lowercase and vice versa, is the first letter a T?
  - IV. Branching task: different tasks for upper and lowercase letters: for capital ones same task as the control/delayed task, for lowercase one same as the dual-task
    - → results: theory confirmed: in fMRI spatial gradient of activation, caudal-rostral direction with branching activating the frontal pole
      - activating only for branching condition

Badre's model=hierarchy driven by control demands→ control resolves competition among alternative representations during action selection, based on control demands and independently from control signals

- The PFC is organised on a rostro-caudal axis based on control demands at increasing levels of abstractions→ control is supported in progressively caudal regions, as decisions are more concrete
- Cognitive control allows us to make decisions about abstract actions (should I call or text my friend?) and to select the concrete motor programs required to produce those actions
    - the frontal lobes are necessary for cognitive control at all levels of abstraction
        - **integrative role** of rostral PFC: consistent with the connectional and cellular anatomy of the frontal pole
    - frontopolar cortex has fewer neurons and neuronal bodies (br. 10) than posterior regions
        - neurons interconnected exclusively with supramodal cortex (associative regions)
        - stellate neurons and not pyramidal: the number of dendritic spines is higher than other cortical areas, but the density of cell bodies is lower
            - less neurons with a richer connectivity, especially with their dendrites: these neurons integrate informations from elsewhere inputs
        - more dendrites branching in high integrative regions (BA 10)
    - hierarchies driven by connectivity: areas can be arranged in a well-defined hierarchy based on their connectivity pattern
        - hierarchy of visual areas in the macaque: at the top there is Br. 8=frontal eye fields
        - feedback control, not unidirectional



- Understanding brain activity and connectivity is fundamental to understand the functions of an area: new in vivo tools, tractography-based parcellation of cortical and subcortical regions in human brains
    - segregation of grey matter from the pattern of connectivity in white matter with other areas
        - ex fronto-polar cortex has no connections with primary sensory areas→ higher integrative functions
    - matching between white matter connectivity and functional connectivity: connections constrain function
    - high correspondence between regions shown by tractography and other techniques (fMRI)
        - in resting state fMRI, synchronisation of BOLD signals=higher connectivity among regions
            - development of highly connected networks like the DMN which sustain processes completely independent from strictly sensory data
- Empirical evidence: 4 tasks:
    - I. Response task: selection of a stimulus-response (S-R) mapping based on a perceptual cue
        - button response depending on the colour of the presented square
    - II. Feature task: selection of a set of S-R mappings based on a perceptual cue→ series of coloured squares containing a single abstract object that varied along one dimension

        - positive vs negative response to different perceptual features depending on the colour of the square
    - III. Dimension task: selection of a set of sets of S-R mappings based on a perceptual cue: series of coloured squares containing two objects
        - match/no-match between them on one dimension, cued by the colour of the square
    - IV. Context task: selection of a set of sets of S-R mappings based on episodic information (current time frame)
        - cues changed meaning according to instructions given at the beginning of the block
        - higher level of abstraction and thus of control demands
    - In such an experiment, Koechlin's and Badre's models lead to different predictions:
        - Cascade model: activity during response, feature and dimension experiments should be confined to posterior frontal regions, since they involve sensory/context control and only context experiment should involve anterior dlPFC
        - control demand model: these experiments should show a rostro-caudal gradient, along with a hierarchical change in the control demand.

Mesulam's model: describes the link between unimodal and transmodal (integrative) areas, based on connectivity info

- Top-down feedback, reciprocal connections=hierarchies
    - represents the convergence of afference and divergence of efference and the possibility of both parallel and serial processing
    - a sensory event could trigger a cascade of processes which get more complex and complete info from the stimulus
- Transmodal/heteromodal areas integrate info from other areas (especially modal ones) in global representations → they account for cognitive operations on different stimuli
- Synaptic architecture allows to lose the stimulus-response bond typical of lower level processes and of lower species=more complex behaviour
    - phylogenetic trend that can explain the emergence of typically human features (ex symbolic language): synaptic connectivity accelerated neuro-cognitive development, the capacity of the single enters a collective culture with will be passed on to next generations, going beyond the Darwinian concept of evolution
        - not only shaped by the environment, but shaping the environment which will influence the next generation
        - "cognition is a trigger for evolution"

The origin and development of gradients and hierarchies in the individual is still debated, in a deep nature vs nurture argument

- Innatist view: brain gradients and hierarchies are innate

  - then how could they be wired up?
- Empiricist view: brain gradients and hierarchies are developed through experience
  - then why do they appear in stereotyped neuroanatomical locations in virtually all humans? There must be a certain level of prespecification

Three gradients

- Unimodal to transmodal regions→ ex Mesula
- Visual to somatomotor
- Task-positive to task-negative
  - task-positive=regions that light up when asked to perform a task with external stimulus