The key takeaways and findings from the abstract are:

1. The traditional homunculus representation is interrupted by regions with distinct connectivity, structure, and function, alternating with effector-specific areas (foot, hand, and mouth).
2. These intervening regions (inter-effector regions) exhibit decreased cortical thickness and strong functional connectivity to each other, as well as to the cingulo-opercular network (CON). The CON is critical for action, physiological control, arousal, error processing, and pain.
3. The structure of intermingling action control-linked and motor effector regions was confirmed in the three largest fMRI datasets. Similar structures were suggested in macaque monkeys and in pediatric fMRI, indicating cross-species homologues and developmental precursors of the inter-effector system.
4. A range of motor and action fMRI tasks showed concentric effector somatotopies (representation of different parts of the body in the brain), separated by the CON-linked inter-effector regions.
5. Inter-effector regions lacked movement specificity and were activated during action planning and axial body movement (like moving the abdomen or eyebrows).
6. Combining these findings with previous studies, the authors suggest M1 contains a system, named the somato-cognitive action network (SCAN), for whole-body action planning.
7. In the M1, two parallel systems intertwine: the effector-specific regions for isolating fine motor control, and the SCAN for integrating goals, physiology, and body movement.

In summary, this research challenges the conventional understanding of M1's organization, proposing a new model that incorporates inter-effector regions involved in broad action planning and body movement integration, alongside effector-specific regions for detailed motor control.

Introduction

1. In the 1930s, Penfield and colleagues mapped the human M1 via direct cortical stimulation. They found that half of the stimulation sites elicited movements, mostly in the foot, hand, and mouth, leading to the concept of a "motor homunculus," which describes a body part representation from head to toe in the M1.
2. Studies in non-human primates showed some discrepancies with this model. M1 was divided into an anterior "old" M1, responsible for gross motor function, and a posterior "new" M1, responsible for fine motor function. The body was represented in anterior M1, while motor effectors like the tail, foot, hand, and mouth were represented in posterior M1. They also suggested a concentric zoning of limbs, with the digits at the center and shoulders at the periphery. As the stimulation moved from posterior to anterior M1, it could elicit increasingly complex, multi-effector actions.
3. The passage also discusses the role of other brain regions in controlling voluntary movements. Activity preceding voluntary movements can first be detected in the dorsal anterior cingulate cortex (dACC), then in the pre-supplementary motor area (pre-SMA), supplementary motor area (SMA), followed by M1. M1 is the main transmitter of motor commands via the corticospinal tract. Other regions like the primary somatosensory cortex (S1), cerebellum, and striatum receive copies of motor commands for correction, learning, and inhibition of competing movements.
4. Functional connectivity mapping studies have identified separate foot, hand, and mouth M1 regions, each with their respective cerebellar and striatal targets. However, these circuits did not include functional connections with control networks that could support the integration of movement with overall behavioral goals.
5. The passage then discusses the usage of precision functional mapping (PFM) with higher resolution and larger amounts of data to map M1 and its connections in greater detail. These results were cross-verified with large scale fMRI studies, and were contextualized in terms of species differences (human vs macaque), developmental stages (neonate, infant, child, adult), and clinical contexts (perinatal stroke).

Two networks alternate in motor cortex (figure 1 & 2)

Discusses findings from a study that used advanced Precision Functional Mapping (PFM) to investigate the organization of the primary motor cortex (M1). Here are the key takeaways:

1. The research revealed two distinct patterns of functional connectivity within the M1, differing from the traditional understanding of M1 as a somatotopic homunculus (a representation of the body's parts). The first pattern corresponded to foot, hand, and mouth representations, with each region connected to its homotopic contralateral M1 and adjacent primary somatosensory cortex (S1). This matched the expected activity during foot, hand, and tongue movements.
2. The second pattern found three areas between the known foot, hand, and mouth regions that were strongly functionally connected to each other, both contralaterally (across hemispheres) and ipsilaterally (within the same hemisphere). These regions formed an interdigitated chain down the precentral gyrus, previously unrecognized and termed the "inter-effector regions."
3. The existence of these inter-effector regions was observed in every highly sampled adult and confirmed with separate data from the same participants. Importantly, this pattern was also found in large group-averaged data from several studies, making it evident across multiple datasets.
4. These inter-effector regions were identified in individuals across various stages of development, appearing in an 11-month-old infant and almost adult-like in a 9-year-old child. They were even identifiable in an individual with preserved motor function who had experienced severe bilateral perinatal strokes damaging large portions of M1.

Inter-effectors link to control network (figure 3)

The passage discusses the functional and structural connectivity of the inter-effector regions in the primary motor cortex (M1) discovered through advanced Precision Functional Mapping (PFM). Here are the key points:

1. The inter-effector regions were found to be interconnected and had functional connections to multiple regions of the cingulo-opercular network (CON), known to be significant for goal-oriented cognitive control. These connections were particularly strong with the supplementary motor area (SMA) and a region in the dorsal anterior cingulate cortex (dACC), but also noticeable with anterior prefrontal cortex (aPFC) and insula.
2. In addition, inter-effector regions were most strongly connected to the dorsolateral putamen in the striatum, centromedian nucleus in the thalamus, and certain cerebellar areas, which are distinct from the effector-specific cerebellar regions.
3. Among all highly sampled individuals, inter-effector regions had stronger connections to CON than the foot, hand, or mouth regions. These connections were stronger to middle insula (known to process pain and interoceptive signals), certain parts of the cerebellum, dorsolateral putamen (critical for motor function), and sensory-motor regions of the thalamus.
4. Notably, the middle inter-effector region showed stronger functional connectivity to the extrastriate visual cortex than the superior and inferior inter-effector regions.
5. The infra-slow resting-state fMRI signals in the CON and the inter-effector network lagged behind those in effector-specific regions, which suggests that high-frequency signals may occur earlier in the CON than in M1, reaching the inter-effectors before the foot, hand, and mouth regions.
6. While the M1 foot, hand, and mouth regions showed strong functional connections with the adjacent primary somatosensory cortex (S1), the inter-effector regions showed lower connectivity with S1. More specifically, their connectivity extended into the fundus of the central sulcus (which represents proprioception), but not to the postcentral gyrus (representing cutaneous tactile stimuli).
7. The brain structure also varied between the inter-effector and effector-specific regions. Inter-effector regions exhibited lower cortical thickness, more similar to the prefrontal cortex, but higher fractional anisotropy (a measure of directional water diffusion in tissues, often used to assess white matter integrity). The myelin content was higher in the inter-effector regions than in foot regions but lower than in hand regions, suggesting different myeloarchitectonic properties.

Concentric motor and body-action zones (figure 3)

The passage discusses an experiment using functional MRI (fMRI) to better understand the functions of inter-effector regions in the primary motor cortex (M1). Here are the key findings:

1. Data was collected from two participants performing 25 different movements, and a novel task involving separate planning and execution phases for coordinated hand and foot movements.
2. The data suggested that the organization of the primary motor cortex is more consistent with a concentric model rather than the traditional homuncular model. This concentric organization suggests concentric zones of activation centered around activation peaks for distal movements (like hands, toes, and tongue), expanding outward for more proximal movements (like shoulder, gluteus, and jaw).
3. These concentric zones intersected in the superior and middle inter-effector regions.
4. Some movements requiring less fine motor control, such as isometric contraction of the abdominals or raising the eyebrow, co-activated multiple inter-effector regions and the cingulo-opercular network (CON). In contrast, movements of the foot and hand only activated corresponding effector-specific regions.
5. Inter-effector regions showed weak movement specificity, with minimal activation differences between preferred and non-preferred movements, and some activation across most movements.
6. Vocalization-related task data showed a dual laryngeal representation confined to the mouth area rather than extending into the inter-effector regions, consistent with the concentric organization model.
7. Regions in CON, known to be involved in action planning, suggest that the connection from CON to the inter-effectors could carry general action planning signals. The inter-effectors showed greater activity during action planning than movement execution in a coordination task involving foot and hand movements, which implies that the implementation of action plans might be facilitated in part by the inter-effector regions in M1.

In summary, these findings support a concentric model of organization within the M1, demonstrate the functional differences between inter-effector and effector-specific regions, and suggest a potential role for inter-effector regions in action planning.

Top of Form

Macaque homologue of body/action network

The passage describes a research study that seeks to link neuroimaging findings in humans to decades of detailed motor mapping in non-human primates, specifically macaques.

Key findings include:

1. Functional MRI (fMRI) studies on macaques revealed foot, hand, and mouth effector-specific functional connectivity patterns that were consistent with those observed in humans.
2. When seeding putative cingulo-opercular network (CON) homologues in the dorsal anterior cingulate cortex (dACC) of macaques, researchers found strong connectivity with the lateral frontal cortex, insula, and supramarginal gyrus - similar to the human CON. They also found connectivity with two regions in the anterior central sulcus that could potentially be homologous to the superior and middle inter-effector regions in humans.
3. Distinct corticospinal connectivity patterns exist in macaques, distinguishing between different regions of their M1. The posterior M1, which is phylogenetically newer, represents the effectors and has a more direct link with fine motor control. The anterior M1, which is older, represents the body, has bilateral connectivity throughout the spinal cord and connects to internal organs. The distribution of adrenal connectivity converges with the proposed inter-effector homologues and connected medial wall regions, such as the supplementary motor area (SMA) and dACC.
4. Direct stimulation studies in macaques have evoked complex, multi-effector actions when longer stimulation trains were applied to the motor cortex. These actions range from feeding behaviours to climbing and defensive postures, and involve coordinated movements that integrate muscles across the foot, hand, and mouth divisions.
5. The inter-effector regions in humans, which are connected to action planning areas and are active during a wide range of foot, hand, and mouth movements, represent potential human homologues to the macaque multi-effector action sites.

In summary, this research provides further evidence of homologous functional connectivity patterns in humans and macaques, suggesting that the inter-effector regions in humans may play a similar role in coordinated, multi-effector actions as observed in macaques.

Effector isolation versus action integration

The passage discusses a new conceptualization of the organizational principle of the motor cortex (M1), moving away from Penfield's nearly 100-year-old homuncular model, which proposed M1 as a continuous map of the human body.

The authors propose a dual-systems, integrate-isolate model of behavioral control, in which effector-isolating and whole-organism action implementation regions alternate. This model better aligns with human imaging data presented in their study, which shows contrasting structural, functional, and connectivity patterns within M1. The inter-effector patterning is said to emerge in infancy and is preserved even in the presence of substantial perinatal cortical injury.

In this new model, the regions for foot, hand, and mouth fine motor skills are organized somatotopically as three concentric functional zones. The distal parts of the effector (toes, fingers, and tongue) are at the center, while the proximal parts (knee, shoulder, and larynx) are on the perimeter. Effector-specific regions show strong activation for preferred movements and are commonly deactivated for non-preferred movements.

The inter-effector regions at the edges of the effector zones coordinate with each other and with the cingulo-opercular network (CON) to perform holistic, whole-body functions in the service of performing actions. This could include action implementation, postural and gross motor control of axial muscles, coordinating breathing with speech and other complex actions, and controlling internal processes and organs, consistent with circuits for whole-body, metabolic, and physiological control.

The authors suggest that these inter-effector regions constitute a somato-cognitive action system (SCAN), working with the CON's upstream executive control operations to coordinate gross movements and muscle groups, control posture and internal physiology, while preparing for and implementing actions. This function aligns with the concept of allostatic regulation, wherein the brain anticipates upcoming changes in physiological demands based on planned actions and exerts top-down preparatory control over the body.

Human electrophysiology evidence

The passage critically revisits Penfield's homunculus model, a representation of the body within the brain, pointing out that it was meant to be an approximation and even Penfield himself described it as an aid to memory where scientific accuracy was impossible. The authors propose that a reexamination of the existing human stimulation data raises doubts about the homunculus in individuals and fits better with their new integrate-isolate model. They suggest a concentric organization, especially in relation to distal-proximal areas, in line with observations in non-human primates. They also point out that face movements can be elicited from areas not traditionally associated with the face according to the homunculus model.

The authors explain that stimulations in the motor cortex often elicit responses that are not just focused on individual movements, but rather suggest a whole-body control system. For instance, subjects have reported the urge to move without actually moving or have moved but denied having done so. They further note that stimulation doesn't usually produce isolated torso or shoulder movements, and often no response is recorded at all.

In a reanalysis of recent studies, they find a region in the motor cortex that never elicited movement, corresponding to the middle inter-effector region of their proposed model. This suggests that typical stimulation strengths might not trigger movements in these regions, akin to higher-order premotor regions.

Lastly, they reference studies involving brain-computer interface (BCI) recordings in M1, which have indicated whole-body movement tuning, potentially supporting the concept of inter-effector activity. They suggest that these inter-effector areas could be a target for whole-body BCI. They mention that speech BCIs have identified the importance of precentral gyrus regions for speech planning, supporting the integrative, whole-body function of the regions identified in their model.

Evidence from clinical neurology

This passage supports the existence of dual systems for movement isolation and action integration in the brain, with some redundancy in the primary motor cortex (M1). Lesions after strokes tend to be unilateral, severely affect distal effectors (such as hands and feet), and do not significantly impact global body control. However, lesions in the SCAN-linked cognitive control network (CON) regions can cause isolated volitional deficits like decreased fluency, abulia, or akinetic mutism, while preserving motor abilities. The passage suggests that anterior and posterior lesions can have different effects, affecting internally generated actions or disrupting execution respectively.

In animals, lesions in M1 usually result in quick recovery of gross effector control, while deficits in fine finger movements persist. This faster recovery may be facilitated by the contra-lesional SCAN circuits taking over proximal functions due to their bilateral spinal cord connectivity. Functions uniquely supported by effector-specific circuitry may be more likely to exhibit persistent deficits.

An individual with extensive bilateral perinatal strokes but normal motor ability showed post-stroke reorganization that maintained SCAN patterning, even at the cost of a portion of the M1 hand area. This suggests the importance of the SCAN for typical motor ability.

The SCAN, connected to thalamic motor nuclei, might be relevant for movement disorders like dystonia or essential tremor. The authors particularly note Parkinson's disease, as many of its symptoms - postural instability, autonomic dysfunction, reduced self-initiated activity, etc., - mirror SCAN's connections to regions relevant for postural control, volition, and physiological regulation.

Similarities to sensory systems

The organizational features of the primary motor cortex (M1) described in the paper have similarities to those found in sensory systems. The concentric somatotopic organization in M1, with fine finger movements at the center, mirrors the organization in the primary visual cortex which over-represents higher acuity processing at the center and transitions to lower acuity in the periphery. The dual-systems model of integrate-isolate in M1 is similar to the parallel and segregated processing streams in visual processing, maintaining different types of information at each level. This is similar to auditory processing in the superior temporal gyrus, which processes acoustic signals in parallel for hearing and speech perception. These findings suggest common organizational principles across the brain’s input and output processing streams. Future work should investigate whether the primary somatosensory cortex (S1) also includes concentric organizational elements.

A network for mind–body integration

The paper suggests that there are two intertwined behavioral control systems in the human primary motor cortex (M1). One system is made up of effector-specific circuits responsible for precise, isolated movements of specialized body parts like fingers, toes, and the tongue, which are used for complex tasks like speaking or manipulating objects.

The second system, called the SCAN (somato-cognitive action system), is more integrative and is involved in whole-body control, integrating motor control, autonomic response, and action planning. The SCAN comprises specific regions in the M1, SMA (supplementary motor area), thalamus, posterior putamen, and postural cerebellum. It is functionally connected to regions linked to free will, movement intentions, and processing of somatosensory, pain, and interoceptive visceral signals.

The SCAN may play a role in complex human-specific actions like coordinating breathing for speech and integrating movements of the hand, body, and eyes for tool use. These various processes require integration to achieve an organism's goals through movement while avoiding injury and maintaining physiological stability, a concept known as allostasis. The SCAN serves as the neural substrate for this integration, facilitating anticipatory changes in posture, breathing, cardiovascular activity, and arousal before an action.

The discovery of this intertwined action and body control in a common circuit could explain why mind and body states are frequently interconnected.