Plasticity based on compensatory effector use in the association but not primary sensorimotor cortex of people born without hands

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What forces direct brain organization and its plasticity? When brain regions are deprived of their input, which regions reorganize based on compensation for the disability and experience, and which regions show topographically constrained plasticity? People born without hands activate their primary sensorimotor hand region while moving body parts used to compensate for this disability (e.g., their feet). This was taken to suggest a neural organization based on functions, such as performing manual-like dexterous actions, rather than on body parts, in primary sensorimotor cortex. We tested the selectivity for the compensatory body parts in the primary and association sensorimotor cortex of people born without hands (dysplasic individuals). Despite clear compensatory foot use, the primary sensorimotor hand area in the dysplastic subjects showed preference for adjacent body parts that are not compensatorily used as effectors. This suggests that function-based organization, proposed for congenital blindness and deafness, does not apply to the primary sensorimotor cortex deprivation in dysplasia. These findings stress the roles of neuroanatomical constraints like topographical proximity and connectivity in determining the functional development of primary cortex even in extreme, congenital deprivation. In contrast, increased and selective foot movement preference was found in dysplastics’ association cortex in the inferior parietal lobe. This suggests that the typical motor selectivity of this region for manual actions may correspond to high-level action representations that are effector-invariant. These findings reveal limitations to compensatory plasticity and experience in modifying brain organization of early topographical cortex compared with association cortices driven by function-based organization.

Significance

What determines the role of brain regions and their plasticity when typical inputs or experience is not provided? To what extent can extreme compensatory use affect brain organization? Is brain organization limited in its plasticity due to strong neuroanatomical constraints? We investigated this question by studying the neural activity profile in primary and association sensorimotor cortices in people born without hands who use their feet to perform everyday manual tasks.

Both animal studies and human cases of deafferentation or amputation have found that the primary sensory and motor cortices reorganize to show activity expansion of adjacent body parts, and that this reorganization is greater when it occurs early in life (1–10).

However, several recent functional neuroimaging studies in people with congenitally missing hands (dysplasic individuals) have stressed the role of experience-based plasticity in the reorganization of the primary sensorimotor hand region. Specifically, it has been proposed that the hand area supports the use of other body parts in performing manual-type, everyday actions, and that this plasticity is not constrained by topographical factors. Results have been reported showing activation of the hand primary sensorimotor cortex for body parts used in place of congenitally missing hands (11, 12). The hand-responsive area in somatosensory cortex of individuals with partially missing hands shrinks depending on the size and use of the hand remains (13, 14). Importantly, in dysplastic individuals, somatosensory stimulation of the foot activated the lateral sensorory cortex (15). Furthermore, in two individuals born without hands bilaterally, it has been shown that strong transcranial magnetic stimulation of the lateral motor cortex generated motor evoked potentials not only in the participants’ residual finger or shoulder but also in the foot. Such stimulation also interfered with performance of a foot motor task (11). These findings were interpreted as evidence for robust plasticity of the sensorimotor cortex and functional takeover of the hand areas by the foot. These studies were interpreted as raising the possibility that the primary sensorimotor cortex is functionally selective rather than selective for a specific body part. On this view, the hand area stands for any effector that functions as a hand in everyday tasks like grasping and manipulating objects (12).

However, the specificity of such supposed compensatory reorganization (for the body part used as hands) has not been thoroughly tested in people born without hands. None of the studies with dysplastic individuals tested whether the hand area is activated more for compensatorily used body parts than for other proximal, but noncompensatorily used organs. Is the hand sensorimotor cortex indeed selective for compensatorily used body parts that serve as effectors? Alternatively, plasticity due to compensatory effector experience may be limited by neuroanatomical
constraints such as topographical proximity and connectivity of this brain system, enabling only a takeover by closer cortical territories or contralateral intact body parts, akin to what is found in late-onset amputation or reanimation.

A related question concerns the effects of missing limbs on the organization of the association sensorimotor action system. Parts of the posterior parietal cortex show preference for specific body parts, specifically the eyes and hands, when participating in goal-directed visuomotor action (16–20). These preferences in the fronto-parietal network also depend on the functional use of body parts such as in the execution of manual tasks like reaching, object manipulation, and grasping (21–25). Given that the foot rather than the hand is the major effector in dysplastics, we additionally tested whether typically hand-selective regions in the parietal and frontal cortex now respond preferentially to the foot, reflecting the effects of effector use-based compensatory plasticity.

We investigated these questions by mapping sensorimotor responses to movement of various body parts in five individuals born without hands who use their feet for everyday functions. The results are discussed in the context of the broader issue of the roles of neural proximity and functional equivalence in shaping the reorganization of primary and association cortices in the absence of relevant sensorimotor experience.

**Results**

To test the specificity of plasticity in the sensorimotor hand areas in people born without arms or hands (SI Appendix, Table S1), we used an active motor paradigm, designed to activate both primary somatosensory and primary motor cortices, similar to previous studies of reorganization (refs. 12 and 26–29; for supporting findings in a passive somatosensory stimulation design, see below). We scanned five dysplastic subjects, as well as a control group, as they performed simple flexing movements of different body parts.

The body parts chosen for this experiment included the hands (in the controls, used as a localizer) and the feet, which the dysplastic subjects are to overcome their disability. Our study participants, according to self-report, rely largely on their dexterous feet (dominantly their right foot; all were right-footed) to perform daily typical manual activities. Their feet are extraordinarily dexterous, allowing them to use cell phones, utensils and nearly all other everyday tools (see list at SI Appendix, Table S2). In a questionnaire of tool use, all of the dysplastic subjects reported using their lower limbs for most of the tools they have used (SI Appendix, Fig. S1). Foot tool use accounted for a minimum of 92% of the used tools, although few tools were jointly manipulated by or remained in specific hands in specific individuals (SI Appendix, Fig. S1 and Table S1). Additionally, we inspected movement of the shoulder and lips, expected to activate neighboring cortical regions on both sides of the missing hand territory, as well as a control body part, which is not an immediate cortical neighbor of the hand and is not used compensatorily to replace hand function as a dexterous effector: the abdomen. While abdominal core muscles may be used to stabilize the body and may thus be used in excess by the dysplastics while using their feet, they cannot be used to replace hand function.

In the control group, this protocol resulted in a typical somatotopic activation pattern with sensorimotor responses along a superior-inferior axis for the foot, abdomen, shoulder, hand, and lips movements (Fig. L4; hand peak is delineated in white), replicating the known Penfield homunculus (30). Topographic responses were found along the central sulcus, postcentral gyrus, and postcentral sulcus, covering Brodmann areas 3a, 3b, and 1 (31), and extending anteriorly from the central sulcus also to the precentral gyrus, covering Brodmann areas 6a, 8, and 12 (32) and potentially parts of the premotor cortex. In the dysplastic subjects, although the peak responses remained topographic along the primary sensorimotor cortex, movement in every tested body part extended toward the deprived area and generated some activation in the hand region (Fig. 1B). This also included increased activation of the primary hand area while they moved their right foot, used by these subjects to perform typical manual actions, as reported before (11, 12). Indeed, plotting the group differences showed that the sensorimotor hand area had stronger activation in the dysplastic subjects than in the controls for moving the various body parts, including the foot (Fig. 1 C and D).

When exploring selectivity of sensorimotor responses, plotting the preferential activation per cortical vertex (in a winner-takes-all approach; Fig. 2 A and B), the dysplastic subjects show a preference for shoulder and abdomen movements in the typical hand area (Fig. 2B; hand area delineated white), which seem to have been displaced and expanded toward the hand area compared with the activation pattern in the controls. This reorganization for the shoulder appears to be similar across the sensory and motor cortices, although a preference for the abdomen is found more anteriorly, in the central sulcus itself, likely originating from the motor cortex. These patterns were consistent across the individual subjects (SI Appendix, Fig. S2) and found also in the right hemisphere for movement of the contralateral body parts (see SI Appendix, Fig. S3 for comparable analyses of the right hemisphere). We further sampled the response pattern within the hand region of interest (ROI). This ROI was defined as significant overlapping sphere for movement of the contralateral body parts (see SI Appendix, Fig. S3) and found also in the right hemisphere for movement of the contralateral body parts (see SI Appendix, Fig. S3 for comparable analyses of the right hemisphere). We further sampled the response pattern within the hand region of interest (ROI). This ROI was defined as significant overlapping sphere for movement of the contralateral body parts (see SI Appendix, Fig. S3 for comparable analyses of the right hemisphere). We further sampled the response pattern within the hand region of interest (ROI). This ROI was defined as significant overlapping sphere for movement of the contralateral body parts (see SI Appendix, Fig. S3 for comparable analyses of the right hemisphere). We further sampled the response pattern within the hand region of interest (ROI). This ROI was defined as significant overlapping sphere for movement of the contralateral body parts (see SI Appendix, Fig. S3 for comparable analyses of the right hemisphere).
Selectivity for the compensatorily used foot in the dysplastics is found in the sensorimotor cortex. However, this selectivity is not found in the primary sensorimotor cortex (PMd), but not in the hand primary sensorimotor cortex, which shows the reverse preference. Movement selectivity comparing the shoulder and foot in the dysplastics shows a robust preference to shoulder movement (a proximal, noncompensatory body part). Preferred body part responses for contraction movements for the dysplastics show a preference for the foot (vs. abdomen movements). Preferred body part responses for contraction movements for the dysplastics show a preference for the foot (vs. abdomen movements).

Foot selectivity in dysplastics (foot > abdomen) is found in the sensorimotor cortex. However, this selectivity is not found in the primary sensorimotor cortex (PMd), but not in the hand primary sensorimotor cortex, which shows the reverse preference. Movement selectivity comparing the shoulder and foot in the dysplastics shows a robust preference to shoulder movement (a proximal, noncompensatory body part). Preferred body part responses for contraction movements for the dysplastics show a preference for the foot (vs. abdomen movements). Preferred body part responses for contraction movements for the dysplastics show a preference for the foot (vs. abdomen movements).

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Therefore, plasticity related to extensive foot use in the dysplasics is found in the association parietal cortex, in the inferior parietal lobule (aIPS), and not in the primary sensorimotor hand area. We also inspected whether functional connectivity (FC) may reflect use-based plasticity within the primary sensorimotor cortex and in the association cortices. The group differences in FC from the hand area across the entire cortex showed FC differences only in the association cortex, in the middle intraparietal sulcus (mIPS; SI Appendix, Fig. S8).

**Discussion**

We tested people born without hands who use their feet to perform everyday manual tasks. We found that their primary sensorimotor hand area is activated by foot movements more than in typically developed control subjects (Fig. 1), replicating previous findings of plasticity in congenital limb absence (11, 12, 15). However, in contrast to previous research, we additionally tested for the selectivity of the compensatorily used effector and found that the hand area shows no foot selectivity. Instead, the hand area is significantly more activated by proximal but noncompensatory body parts, such as the shoulder and abdomen, which are not used as dexterous effectors (Fig. 2). In the association sensorimotor cortex, we found evidence for compensatory plasticity specific to the foot. Foot selectivity in the aIPS and inferior parietal lobule (Fig. 2 D, E, and G) was found exclusively in the dysplasic participants.

Past findings of primary sensorimotor plasticity in people born without hands were thought to reflect use-dependent, compensatory plasticity for sensorimotor loss (11, 12, 15). Those results were interpreted as evidence that the primary sensorimotor cortex shows functional selectivity for performance of tasks typically conducted with the hands, and not necessarily for the specific body part (12). This interpretation builds on a model based on the organization of association sensory cortex in congenital blindness and deafness. In these cases, the role of association sensory cortices appears to be defined not strictly by their typical sensory modality, but as input (e.g., sensory loss, effector function). This was demonstrated for high-level visual cortex in the blind where domain selectivity was found for distinct object domains, including artifacts, body parts, and scenes (36–42) with nonvisual stimuli. Similar results were obtained for nonvisual spatial localization (42) and motion perception (43). Analogous results of retained functional specialization independent of modality of input have been found for the deaf (44–46). These findings encouraged the view that the observation of seemingly compensatory reorganization in people born with partial dysplasia is driven by similar use-dependent, compensatory plasticity. However, the topographical nature of the early sensory and motor cortices. Specifically, we found selectivity for foot movement compared with movement of the abdomen and shoulder in parts of the inferior parietal lobule, mainly in the anterior IPS area, bordering the postcentral sulcus and, to some extent, in the angular/supramarginal gyrus (2 B, D, and E). We also found increased FC from the primary sensorimotor hand area to IPS, albeit in a more posterior region, in mIPS (SI Appendix, Fig. S8B).

The strongest result was found in the aIPS and, inferiorly to it, in the inferior parietal lobule, falling with high probability within several cytoarchitectonic areas, from BA2 to hIP2 and PF1. Electrophysiological data in nonhuman primates and fMRI data in humans have shown that these regions support various types of manual behaviors. These include visually guided object manipulation, tool use and grasping movements (23, 25, 59–62), action observation and imitation (63), and additional more abstract action representations of function and goal (64, 65). Therefore, this region’s motor selectivity for the foot may be functional and related to compensatory use, linking it to a role in representing effector-invariant/effector-independent action; i.e., related to any body part used as an effector.

Whereas several studies have shown effector-invariant action representations in the parietal lobe with regard to hand laterality and correspondence between hand and eye (66–69), generally in mIPS and pIPS, aIPS shows effector selectivity for the hand, compared with foot or eye movements (70). Importantly, aIPS...
appears to support grasping actions not only with the hands but also with tools (71–74). Our findings would therefore suggest that this region’s role may have to do with the use of the hands or tools as effectors, enabling it to also extend its selectivity to the foot, when it is used as an effector throughout life.

Thus, the current study shows a clear division in organization principles between the primary, topographic cortices, and the association cortex. We find that these regions differ in their compensatory plasticity and in the manner in which experience can affect their organization. In the primary sensorimotor cortex, we find that similarly to the lesion-induced map plasticity in late-onset animal and human studies, even congenital deprivation and compensatory use cannot overcome neuroanatomical constraints such as the topographical identity and connectivity, which determine the functional development of these brain regions. In contrast, functional specialization occurs at relatively high levels of representation in the parietal lobe of the dysplasics. Analogously to the case of the association cortices of the blind and deaf, the aIPS in dysplasics appears to show effector-invariant plasticity and selectivity—to the foot in this case. This suggests its role extends beyond the hand to support object manipulation with other bodily effectors.

Methods

Participants. Five individuals born with severely shortened or completely absent upper limbs (individuals with upper limb dysplasia: dysplasias 1–5), and eight typically developed control subjects, matched for age (no group difference; P < 0.25) participated in the experiment. The causes of dysplasia were genetic, teratogenic medications (thalidomide), or unknown. See SI Appendix, Table S1 and Supplemental Methods for the summary of the characteristics of the dysplasias, as well as images of their residual limbs. None of the dysplasias had a history of phantom limb sensations or movements, and all were adept at performing everyday actions and tool use with their feet (see SI Appendix, Table S2). All of the dysplastic participants used their right foot dominantly. None of participants had a history of psychiatric or neurological disorder. They gave written informed consent in accordance with the institutional review board of Harvard University, which approved all of the experiments.

Experimental Design. The motor experiment was carried out in a block design fMRI experiment. Mouth, abdomen and either side hands (for the control subjects), shoulders, and feet were moved (simple flexing/contraction movement) in separate blocks (6 s movement and 6 s rest) in randomized order according to an auditory cue (metronome). Four flex and relax movements were performed in each block at a frequency of 0.66 Hz. Due to our focus on the compensatory use of the feet, and as all of the dysplastic participants were dominantly right-footed, we used the movements of the right hand and foot for further examination and provide evidence for similar organization of the right hemisphere in response to left hand and foot movement in SI Appendix, Fig. S3. A supplementary somatosensory experiment with four of the five dysplastic subjects was carried out in a block design fMRI experiment (see acquisition detail and detail of the paradigm in SI Appendix, Supplemental Methods).

Functional Imaging. The blood oxygen level-dependent (BOLD) fMRI measurements were obtained in a Siemens Trio 3-T scanner at the Center for Brain Science at Harvard University. For acquisition detail, see SI Appendix, Supplemental Methods. The main experiment had three runs of 186 whole-brain images each collected in one functional scan. Separate 3D recordings for the simultaneous multislice echo-planar imaging (SMS-EPI) sequence, Steven for modifications that enabled imaging of the hand sensorimotor cortex (delineated in white in Figs. 1 and 2) was defined based on the body part whose movement elicited the highest activation across the group (Fig. 2 A and B). The same analyses were performed for the somatosensory supplemental experiment (SI Appendix, Fig. S4). Group analyses in the control group were conducted in a hierarchical random effects analysis (RFX GLM; ref. 77) and, in the dysplasias, a fixed-effects approach to the group analyses in the control group. For group level somatotopic preferential mapping, each cortical vertex is colored based on the body part whose movement elicited the highest activation across the group (Fig. 2 A and B). The same analyses were performed for the somatosensory supplemental experiment (SI Appendix, Fig. S4). Group analyses are presented on the Colin27 brain inflated (or folded; SI Appendix, Fig. S6) cortices, to which individual surface (cortical) data were aligned based on the curvature patterns. To link our findings to the anatomic characterization of these regions, activation for some of the conditions was overlaid on the probabilistic cytoarchitectonic atlas (33–35, 78) (SI Appendix, Figs. 56 and 57). All areas defined by these maps are shown at 40% probability of belonging to this cytoarchitectonic region. Group comparisons were conducted using both frequentist (t test and mixed effects ANOVA; with group and body part factors; Figs. 1D and 2F and SI Appendix, Fig. S3F) and sensitive Bayesian analyses (refs. 79 and 80, Figs. 1C and 2H and SI Appendix, Figs. S3G and S8B), appropriate for testing small samples of unique populations and patients. See detail of the Bayesian analyses in SI Appendix, Supplemental Methods. Bayesian factor (BF) of over 3 is considered substantial evidence and BF over 10 is considered strong evidence against the null hypothesis (79), in our case suggesting a group difference. The data generated and analyzed for the current study are available from the corresponding author upon request.

FC. A dataset of spontaneous BOLD fluctuations for the investigation of intrinsic (rest state; ref. 81) FC was collected while the subjects lay in the scanner with no external stimulation or task. For details, see SI Appendix, Supplemental Methods.

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