OXFORD

Cerebral Cortex, 2023, **33**, 6862–6871
https://doi.org/10.1093/cercor/bhad006
Advance access publication date 21 January 2023
Original Article

Gravity matters for the neural representations of action semantics

Ziyi Xiong[1,2,†], Yu Tian[3,4,†], Xiaosha Wang[1,2,*], Kunlin Wei[4,5,6,*], Yanchao Bi[1,2,7]

[1]State Key Laboratory of Cognitive Neuroscience and Learning & IDG/McGovern Institute for Brain Research, Beijing Normal University, Beijing 100875, China,
[2]Beijing Key Laboratory of Brain Imaging and Connectomics, Beijing Normal University, Beijing 100875, China,
[3]National Key Laboratory of Human Factors Engineering, China Astronaut Research and Training Center, Beijing 100094, China,
[4]School of Psychological and Cognitive Sciences, Peking University, Beijing 100871, China,
[5]Beijing Key Laboratory of Behavior and Mental Health, Beijing 100871, China,
[6]Peking-Tsinghua Center for Life Sciences, Peking University, Beijing 100871, China,
[7]Chinese Institute for Brain Research, Beijing 102206, China

*Corresponding authors: Xiaosha Wang, State Key Laboratory of Cognitive Neuroscience and Learning & IDG/McGovern Institute for Brain Research, Beijing Normal University, Beijing 100875, China. E-mail: wangxiaosha@bnu.edu.cn and Kunlin Wei, School of Psychological and Cognitive Sciences, Peking University, Beijing 100871, China. E-mail: wei.kunlin@pku.edu.cn

†Ziyi Xiong and Yu Tian are co-first authors

The dynamic relationship between the neural representation of action word semantics and specific sensorimotor experience remains controversial. Here, we temporarily altered human subjects' sensorimotor experience in a 15-day head-down tilt bed rest setting, a ground-based analog of microgravity that disproportionally affects sensorimotor experiences of the lower limbs, and examined whether such effector-dependent activity deprivation specifically affected the neural processes of comprehending verbs of lower-limb actions (e.g. to kick) relative to upper-limb ones (e.g. to pinch). Using functional magnetic resonance imaging, we compared the multivoxel neural patterns for such action words prior to and after bed rest. We found an effector-specific (lower vs. upper limb) experience modulation in subcortical sensorimotor-related and anterior temporal regions. The neural action semantic representations in other effector-specific verb semantic regions (e.g. left lateral posterior temporal cortex) and motor execution regions were robust against such experience alterations. These effector-specific, sensorimotor-experience-sensitive and experience-independent patterns of verb neural representation highlight the multidimensional and dynamic nature of semantic neural representation, and the broad influence of microgravity (hence gravity) environment on cognition.

Key words: action verb; fMRI; microgravity; semantics; sensorimotor experience.

Introduction

How plastic are semantic neural representations? Are common word meanings that have been already acquired still constantly updated as a result of our constant experiential streams? One of the central issues in the enterprise of semantic research is indeed the extent and nature of the involvement of sensorimotor experiences in semantic representation: whether and how the neural representation of the meaning of the word "kick" entails, relies on and/or is satisfied by the sensorimotor experiences associated with the action of *kicking*. As one of the cornerstones of embodied cognition (e.g. Pulvermüller 2005; see critical discussions in Caramazza et al. 2014), it has been consistently observed, based on neuroimaging, that the comprehension of action words elicits activation in distributed brain regions, including the primary sensorimotor cortex (M1 and S1) and dorsal premotor cortex (PMd), which directly support motor execution (Hauk et al. 2004; Lin et al., 2015a; Tettamanti et al. 2005; Willems et al. 2010), and those assumed to be related to higher order motor action in a more abstract manner, such as the left lateral posterior temporal cortex (LPTC; see Wurm and Caramazza 2021 for review), left inferior frontal gyrus (IFG) and supplementary motor area (SMA; Warburton et al. 1996; Bedny et al. 2008; Yu et al. 2011; Yang et al. 2017). Motor system impairments [e.g. in Parkinson's disease (PD; Fernandino et al. 2013a) or via transcranial magnetic stimulation (TMS)] have been found to modulate action verb judgment behaviors, although the effect directions have been inconsistent in TMS studies (inhibitory for TMS on M1 in Repetto et al. 2013; Vukovic et al. 2017; and Vukovic et al. 2021; faciliatory for TMS on PMd in Willems et al. 2011). While these classical findings suggest that certain brain regions are related (or even causal) to semantic behavioral processing of action words, they do not constitute direct evidence for how sensorimotor experience dynamically modulates semantic neural representations, given how such brain regions may have functions beyond specific sensorimotor processes (i.e. suffering the risk of reverse inference fallacy; see Poldrack 2006).

Only a few fMRI studies have examined the role of sensorimotor experience in the neural representation of action word meaning, focusing on motor experience enrichment and yielding inconclusive results. For instance, ice hockey playing experience has been demonstrated to increase PMd activity and decrease M1/S1 activity when listening to hockey-related sentences (Beilock et al. 2008; Lyons et al. 2010). Relatedly, higher accuracy after learning physics concepts (e.g. angular momentum) through hands-on action (compared with observation of wheel-manipulation consequences) is mediated by greater activation in M1/S1 when understanding words denoting physical concepts (Kontra et al. 2015). That is, the neural activities of action-related words in primary and association sensorimotor cortices, not in more abstract verb-semantic regions (e.g. LPTC), have been reported to change with

Received: November 28, 2022. **Revised:** December 31, 2022. **Accepted:** January 2, 2023
© The Author(s) 2023. Published by Oxford University Press. All rights reserved. For permissions, please e-mail: journals.permission@oup.com.

Downloaded from academic.oup.com/cercor/article/33/11/6862/6995384 by guest on 23 September 2026

motor experience enrichment, yet the directions of the results were not consistent across studies. The complexity of the result patterns might be related to the fact that these studies entail complex action experiences and that the effects of multiple kinds (e.g. complex personal spatial/temporal interactions associated with ice hockey) were entangled. Besides motor areas, recent evidence reported that learning new words associating with movement sequences (action verb learning) induced rapid neuroanatomical plasticity in regions related to general semantic processing, including left anterior temporal lobe (ATL; Vukovic et al. 2021). Furthermore, for regions representing action semantics in multivoxel activity patterns abstracted away from modality and/or exemplars (e.g. LPTC; Wurm and Caramazza 2021), it is necessary to adopt multivoxel pattern analyses to test the possibility that the effects of motor experience on their neural representations of action verbs may be reflected in activation patterns.

Here, we took advantage of an unusual setting that introduces short-term alteration of sensorimotor experience in an effector-specific way: the 15-day, 6° head-down tilt bed rest experiment (HDBR). Such an operation simulated the working environment in outer space and substantially deprived the subjects' lower-limb action sensorimotor experience (e.g. walking, standing, stomping) more radically than actions performed by the upper limbs (e.g. grasping, reaching, object manipulation), which were not constrained. This paradigm has been widely used to study the effects of gravity on human cognitive functions (e.g. biological motion perception; Wang et al. 2022). Does the more radical lower-limb sensorimotor experience alteration specifically affect how the brain represents the meanings of lower-limb action verbs (e.g. to stomp)? Given that effector-specificity is the most fundamental principle for the neural organisations of the sensorimotor systems, answering this question allows us to test the level of representation specificity in which semantic neural representation relies dynamically on one's sensorimotor experience. Evidence of lower-limb motor short-term experience change leading to changes in neural representation for common foot action verbs (to stomp, to kick) would indicate effector-specific motor dynamic "grounding" for the corresponding representation; for those regions whose word meaning representation is independent of specific motor experience modulation, either because such knowledge becomes fully abstracted once acquired (despite knowledge acquisition requiring motor experience), or because the knowledge is not derived from sensorimotor experiences, they are not predicted to be influenced by temporary motor experience manipulation.

Materials and methods

Subjects and HDBR experiment procedure

Twenty-four healthy human subjects were recruited for the 15-day, 6° head-down tilt bed rest (HDBR) experiment. They were admitted to the Space Science and Technology Institute (Shenzhen) 7 days before the start of HDBR and were released 8 days after the HDBR. During the HDBR experiment, they remained in the head-down tilt position all of the time (no exceptions for daily routines like meals and bathing). The functional actions of lower-limbs, including body-weight bearing, locomotion, coordination actions to support upper-body actions, were practically absent. Manual actions such as stretching the arm or browsing the phone with fingers remained unrestricted. All subjects were native Mandarin Chinese speakers who were right-handed and had no history of neurological or psychiatric disorders.

All subjects except for one (with only post-HDBR fMRI data) were scanned before (pre-) and after (post-) HDBR. Therefore, 23 subjects (all males; age: $M \pm SD = 27.9 \pm 3.4$ years, range: 24–35 years) with acceptable head motion (< 3 mm maximum translation or 3° rotation) were included in the analysis of the verb judgment experiment.

This study was approved by the Human Subject Review Committee at the Space Science and Technology Institute (Shenzhen) and was conducted in accordance with the Declaration of Helsinki. All subjects provided informed consent and received monetary compensation for their participation.

fMRI experimental design and stimuli

We carried out a verb judgment fMRI task to evaluate the effects of HDBR on the neural representations of action semantics. The target stimuli of this task were two salient hand action verbs ("抓",/zhua1/, to scratch; "捏",/nie1/, to pinch) and two salient foot action verbs ("踩",/cai3/, to stomp; "踢",/ti1/, to kick). The four target verbs were matched in terms of word frequency (logW: "抓" = 3.93, "捏" = 2.53, "踩" = 3.02, "踢" = 3.36; Cai and Brysbaert 2010). Two mouth action verbs ("咬",/yao3/, to bite; "舔",/tian3/, to lick) were included as oddball trials. Our study belongs to a larger neuroimaging project in the special HDBR setting with limited scanning time. Choosing a small number of good quality stimuli for each condition leaves room for more repetitions and has been shown to be able to establish reliable item-specific activation patterns, which allows for comparisons within and between conditions (e.g. see Coutanche and Thompson-Schill 2015; Wang et al. 2018). During the experiment, subjects were asked to listen to the spoken names of these action verbs and to press a button when they heard a mouth-related action verb (Fig. 1a). The task was scanned in one run that lasted 336 s. The run consisted of 64 target trials (1-s auditory word, followed by 2-s silence), 16 oddball trials (1-s auditory word, followed by 2-s silence; eight times for each mouth-related verb) and 32 null trials (3-s silence). The four target action verbs were grouped in random order in blocks and repeated 16 times. The oddball and null trials were pseudo-randomly interposed between the target trials. The run started with 12-s silence and ended with 12-s silence. The stimulus order was randomised for each subject in the pre-HDBR scan and was repeated for the same subject in the post-HDBR scan. In both the pre-HDBR and post-HDBR scans, subjects showed high accuracies of oddball detection (pre-HDBR: $M \pm SD = 88\% \pm 17\%$; post-HDBR: $M \pm SD = 89\% \pm 16\%$), suggesting that they were attentive during the task.

Image acquisition and preprocessing

Functional and structural MRI data were collected from a 3-T Siemens Trio Tim Scanner at the Shenzhen Institute of Advanced Technology MRI Center (1 day before and after the HDBR procedure). For structural MRI, high-resolution anatomical three-dimensional magnetisation-prepared rapid gradient (3D-MPRAGE) images were collected in the sagittal plane (192 slices, repetition time (TR) = 2530 ms, echo time (TE) = 2.96 ms, flip angle (FA) = 7°, matrix size = 256 × 256, voxel size = 1 × 1 × 1 mm^3). Functional MRI data were collected using an epoch-planar imaging sequence that covered the whole cerebral cortex and the cerebellum (38 axial slices, TR = 2000 ms, TE = 30 ms, FA = 90°, matrix size = 64 × 64, voxel size = 3 × 3 × 3 mm^3 with a gap of 0.45 mm).

All data were preprocessed using Statistical Parametric Mapping software (SPM 12; RRID: SCR_007037; https://www.fil.ion.ucl.ac.uk/spm). For each subject, the first four volumes of each

Downloaded from academic.oup.com/cercor/article/33/11/6862/6995384 by guest on 23 September 2026

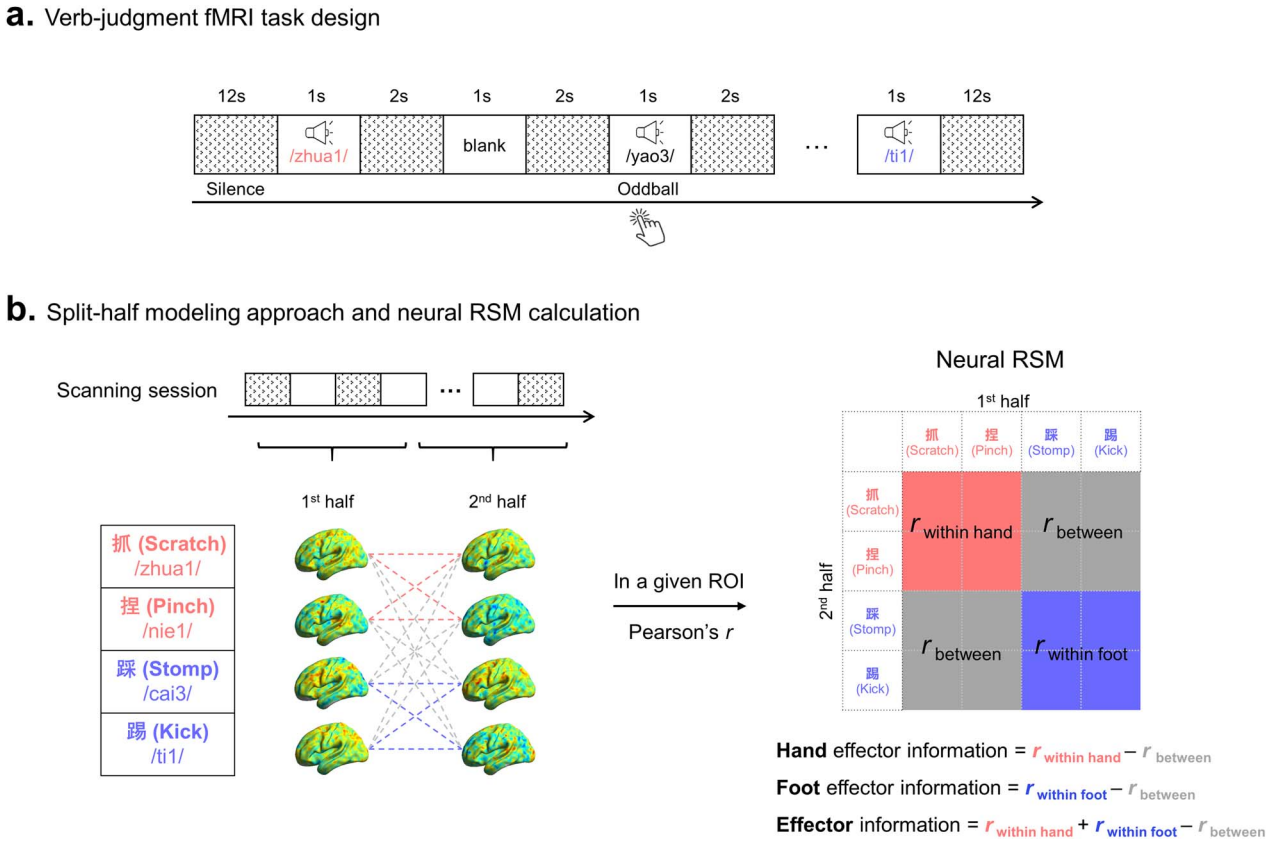

Fig. 1. Experimental design and analysis procedure. (a) Verb-judgment task fMRI design. Subjects were asked to think about the meanings of the action verbs they heard, and to press the key when a mouth action verb is heard (oddball trials). (b) Analysis pipeline of multivoxel pattern correlation analysis. For each of the four target words, we calculated its whole-brain *t* map in the first and second half of the functional run (based on eight repetitions in each half). For a given ROI, we computed Pearson's correlation between the two halves for each pair of words to generate the neural RSM shown in the right panel. Three types of effector information were then calculated from the neural RSM.

run were discarded for signal equilibrium. The remaining images underwent slice timing and head motion correction and were then spatially normalised into the Montreal Neurological Institute (MNI) space using unified segmentation (resampled into 3-mm isotropic voxels). For multivoxel pattern analyses, the functional images were spatially smoothed using a 3-mm full width at half-maximum (FWHM) Gaussian kernel. For univariate analyses, the functional images were spatially smoothed with a 6-mm FWHM Gaussian kernel.

Multivoxel pattern analysis

Generalised linear model

For multivoxel pattern analyses of the verb judgment experiment, the preprocessed functional data were analyzed using a generalised linear model (GLM), which was built in a split-half approach (Haxby et al. 2001; Haushofer et al. 2008). That is, as each target action verb repeated 16 times in the run, each of them was modeled with two regressors corresponding to the first eight onsets or the last eight onsets. This way of separating fMRI data into two halves was adopted to reduce the influence of temporal collinearity in pattern similarity analyses (Mumford et al. 2014). A regressor corresponding to oddball trials (i.e. mouth-related verbs) was also included, and each of these regressors was convolved with a canonical hemodynamic response function. The GLM further included six predictors of head motion parameters. A high-pass-filter cutoff was set at 128 s. After model estimation, we calculated the whole-brain *t* maps of each target verb relative to baseline in the first or second half of the run for further multivoxel pattern correlation analyses.

Information representation computation

For a given region of interest (ROI), the voxel-wise *t* values for each action verb in the first or second half of the run were extracted and correlated between the two halves (Pearson's correlation). This resulted in an asymmetric 4×4 neural representational similarity matrix (RSM), with diagonal values reflecting the neural pattern stability of each action verb and off-diagonal values reflecting the neural pattern similarity between pairs of action verbs. After Fisher-z transformation of this RSM, as shown in Fig. 1(b), we then computed the hand and foot information as the differences between the averaged Pearson's *r* values within each action effector and the averaged Pearson's *r* values between action effectors (i.e. between hand and foot verbs), respectively. We also calculated the effector information as the average of hand and foot information to functionally localise effector-specific verb semantic regions (see below). Note that the "information" defined here included diagonal values to capture the identity information of single action verbs.

ROI definition

We defined three types of ROIs: (i) *effector-specific verb semantic regions* were functionally defined as regions showing significant effector information (average of hand and foot information, which was calculated as the differences between all within-effector values and all between-effector values in neural RSMs) in a

Downloaded from academic.oup.com/cercor/article/33/11/6862/6995384 by guest on 23 September 2026

whole-brain searchlight analysis using the pre-HDBR data (see Supplementary Methods for details). Six clusters were found at the threshold of voxel-level one-tailed $P < 0.005$, cluster-level family-wise error (FWE) corrected $P < 0.05$ (Table S1 and Fig. 2a, upper panel). The cluster-forming threshold of $P < 0.005$ was adopted here to reduce false-negatives, as we only had four action verbs. Three out of six clusters (i.e. the left pIPS, left SMA/PMd and vmPFC) also survived the conventional threshold of voxel-level $P < 0.001$, cluster-level FWE-corrected $P < 0.05$, and yielded similar verb effector × HDBR training interaction effects with the results reported in the main text. (ii) The *general semantic region, left ATL* (Fig. 2b, left panel), was defined anatomically as a union of the following six anterior temporal regions in the Harvard-Oxford Atlas (probability > 0.2, following Xu et al. 2018): the temporal pole, the anterior superior temporal gyrus, the anterior middle temporal gyrus, the anterior inferior temporal gyrus, the anterior temporal fusiform cortex and the anterior parahippocampal gyrus. (iii) M1/S1 *motor execution regions* (Fig. 2c, left panel) were functionally defined by contrasting foot versus hand actions in a motor execution-imagery experiment carried out after the verb-judgment task prior to HDBR (see Supplementary Materials for details).

ROI-level verb effector × HDBR training interaction effects

In each ROI we defined above, the voxel-wise t values for each action verb were extracted to compute the hand and foot information, respectively. These values were examined using repeated-measures analyses of variance (ANOVAs), with verb types (hand, foot) and HDBR training (pre-HDBR, post-HDBR) as the within-subject factors. For effector-specific verb semantic regions, the significance was corrected for multiple ROIs ($n = 6$) using the Bonferroni method. For regions showing nonsignificant verb effector × HDBR training interactions ($P > 0.05$), a Bayesian repeated-measures ANOVA was conducted using JASP software (RRID: SCR_015823; https://jasp-stats.org/ (JASP Team 2022)) with a default setting (r scale fixed effects = 0.5, r scale random effects = 1, r scale covariates = 0.354, posterior samples and numerical accuracy = Auto). The effects of the interaction were calculated by comparing across the matched models, as suggested by van den Bergh et al. (2020).

Whole-brain verb effector × HDBR training interaction effects

To uncover additional regions whose verb neural semantic representation was potentially modulated by specific alteration of action experience, we tested the interaction effects between the verb effector (hand, foot) and the HDBR training (pre-HDBR, post-HDBR) using a whole-brain searchlight analysis (Kriegeskorte et al. 2006). For each voxel in the brain, we built a 9-mm-radius spherical ROI (containing 123 voxels) and calculated the hand and foot information separately. We assigned the resulting information value to the center voxel of each spherical ROI. In this way, we generated whole-brain maps of hand and foot effector information for each subject in both the pre- and post-HDBR fMRI data. We then carried out repeated-measures ANOVAs, with verb types (hand, foot) and HDBR training (pre-HDBR, post-HDBR) as within-subject factors. Specifically, we calculated the differences between the foot and hand information for each subject at each time point, applied spatial smoothing (FWHM = 6) to these maps, and compared the pre- and post-HDBR maps across subjects using the F test. The verb effector × HDBR training interaction F map was thresholded at voxel-level $P < 0.001$, cluster-level FWE-corrected $P < 0.05$. We also performed a whole-brain searchlight analysis using 12-mm-radius spheres, which revealed the same significant clusters with larger sizes.

Resting-state functional connectivity analysis

To examine the possible functional coupling between the clusters showing verb effector × HDBR training interaction effects, we carried out the *resting-state functional connectivity (rsFC) analysis*. rsFC patterns between the clusters were calculated in an independent group of 144 healthy subjects (data from Yang et al. 2017). They were all right-handed, native Mandarin speakers with no history of neurological or psychiatric disorders. This study was approved by the Institutional Review Board of the National Key Laboratory of Cognitive Neuroscience and Learning, Beijing Normal University, and each subject provided informed consent. During the resting-state scan (lasting 6 min and 40 s), subjects were instructed to stay awake and keep their eyes closed. The preprocessing steps of the resting-state data included discarding the first 10 time points, slice timing, head motion correction, spatial normalisation to MNI space using unified segmentation (resampling into 3-mm isotropic voxels), linear trend removal, bandpass filtering (0.01–0.1 Hz), spatial smoothing (FWHM = 6) and regressing out the nuisance covariates, including rigid-body six head motion parameters, white matter signal, cerebrospinal fluid signal and the global signal. Seed-based functional connectivity was computed with the Resting-State fMRI Data Analysis Toolkit (REST; RRID: SCR_009641; http://www.restfmri.net, Song et al. 2011). We used clusters surviving in the aforementioned whole-brain searchlight analysis of verb effector × HDBR training interaction effects as seeds and generated their whole-brain connectivity maps by correlating the mean time series of the seed ROI with the time series of every other voxel in the brain for each subject. The r maps were then Fisher-z transformed and averaged across subjects to produce a group-level functional connectivity map, which was thresholded at voxel-level FWE-corrected, one-tailed $P < 0.05$, cluster size > 50 voxels.

Brain visualisation

The surface-view brain results and ROIs were produced using BrainNet Viewer (RRID: SCR_009446; https://www.nitrc.org/projects/bnv/, Xia et al. 2013) with the "nearest voxel" mapping algorithm on a standard MNI space brain surface. The multi-slice view brain results were produced using MRIcroGL (RRID: SCR_002403; https://www.nitrc.org/projects/mricrogl).

Results

The 15-day HDBR procedure mimicking the microgravity condition may introduce broad cognitive-neural changes, including brain structural plasticity in the prefrontal and parietal regions (Koppelmans et al. 2017), vestibular neural processing (Yuan et al. 2018) and biological motion perception (Wang et al. 2022). The core question of our study is whether verb neural semantic representation is modulated by specific action deprivation, as evidenced by the verb effector × HDBR training interaction, which could not be attributed to general effects of HDBR and/or a practice effect. For the two foot action verbs (*to kick* and *to stomp*) and the two hand action verbs (*to scratch* and *to pinch*) that we took as stimuli, we first correlated their neural activity patterns to construct neural RSMs and then computed the hand or foot information as the differences between Fisher-transformed Pearson's r values between the action verbs operated by the same effector and the action verbs operated by different effectors. As expected, the within-effector

Downloaded from academic.oup.com/cercor/article/33/11/6862/6995384 by guest on 23 September 2026

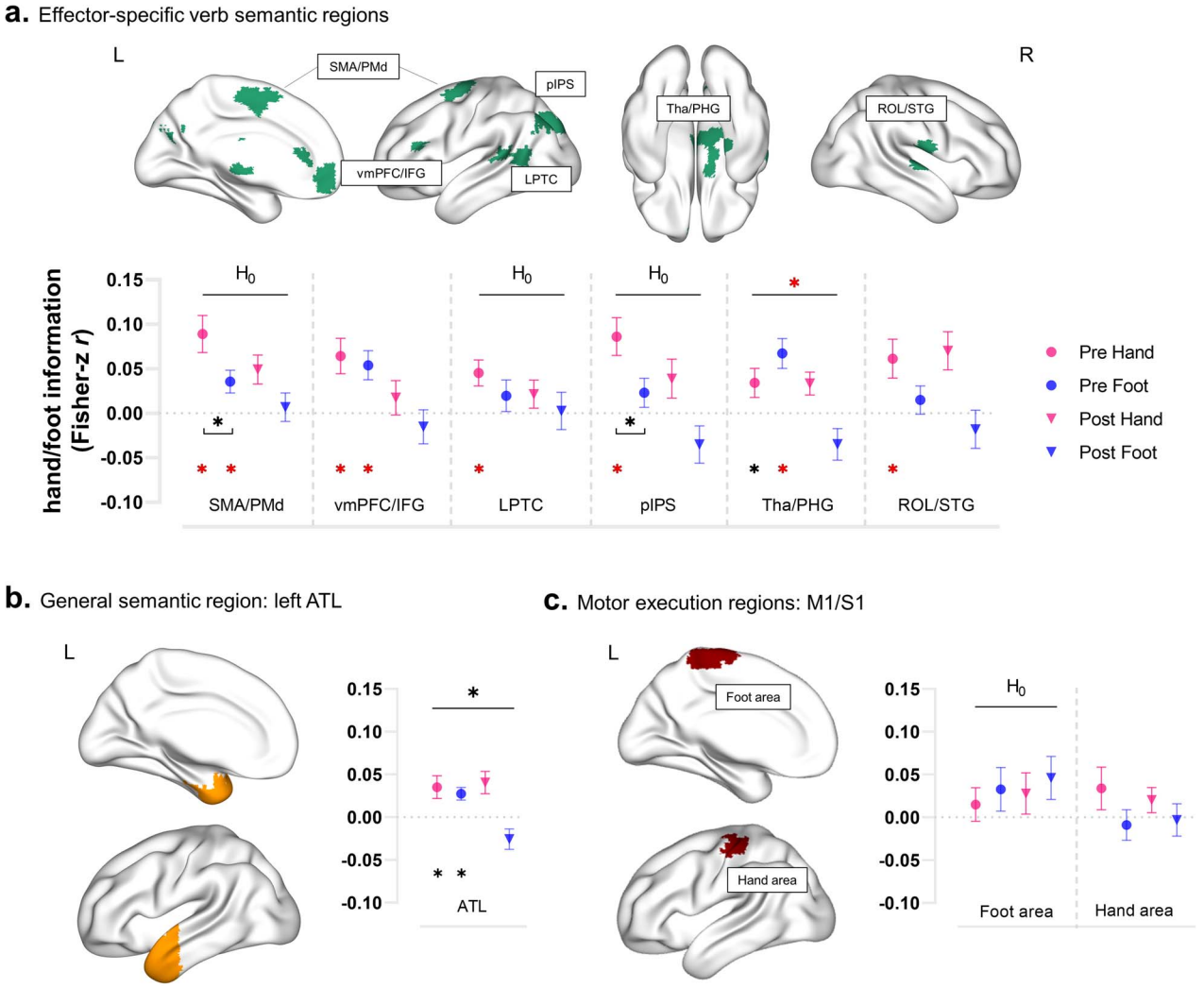

Fig. 2. ROI-level results of verb effector (hand, foot) × HDBR training (pre-HDBR, post-HDBR) interaction effects. (a) Effector-specific verb semantic regions were functionally localised in a whole-brain searchlight analysis in pre-HDBR (thresholded at voxel-level one-tailed $P < 0.005$, cluster-level FWE-corrected $P < 0.05$). (b) The general semantic region, the left ATL, was anatomically defined based on the Harvard-Oxford atlas (following Xu et al. 2018); (c) M1/S1 motor execution regions were functionally defined by contrasting foot and hand actions in a motor execution-imagery fMRI task obtained from the same group of subjects (thresholded at voxel-level FWE-corrected $P < 0.05$, cluster size > 50 voxels). Error bars indicate the standard error. Lines above the graphs indicate the significance level of interaction effect. Asterisks in black indicate uncorrected $P < 0.05$ and asterisks in red indicate Bonferroni-corrected $P < 0.05$ (number of corrections = 6). H_0: Bayesian tests showing moderate evidence for the absence of verb effector × HDBR training interaction effect ($BF_{incl} < 0.33$). L: left; R: right; SMA: supplementary motor area; PMd: dorsal premotor cortex; vmPFC: ventromedial prefrontal cortex; IFG: inferior frontal gyrus; LPTC: lateral posterior temporal cortex; pIPS: posterior intraparietal sulcus; Tha: thalamus; PHG: parahippocampal gyrus; ROL: Rolandic operculum; STG: superior temporal gyrus; ATL: anterior temporal lobe; M1/S1: primary sensorimotor cortex.

verb pairs were judged to be semantically more similar than the between-effector verb pairs (semantic similarity rating from 31 college students, 1–7 scale: $M_{within} = 5.05$ vs. $M_{between} = 1.74$, $t(30) = 16.42$, two-tailed $P < 0.001$, Cohen's $d = 2.95$). Below we first report ROI-level verb effector × HDBR training interaction results in three types of ROIs: effector-specific verb semantic regions, the left ATL and the M1/S1 motor execution regions. We further carried out a whole-brain searchlight analysis to uncover other potential regions with similar interaction effects, and explored functional coupling between these regions using rsFC analysis.

ROI-level results of verb effector × HDBR training interactions

Effector-specific verb semantic ROIs

These regions (Fig. 2a, upper panel) were functionally defined as regions showing significant effector information (average of hand and foot information) in a whole-brain searchlight analysis (Kriegeskorte et al. 2006) using the pre-HDBR data. The following regions survived the threshold of voxel-level $P < 0.005$, cluster-level FWE-corrected $P < 0.05$: the left SMA/PMd, the ventromedial prefrontal cortex (vmPFC) extending to the left IFG, the left LPTC, the left posterior intraparietal sulcus (pIPS), subcortical areas extending from the right thalamus (Tha) to the brainstem and to the right parahippocampal gyrus (Tha/PHG), and a cluster encompassing the right Rolandic operculum and the adjacent superior temporal gyrus (ROL/STG) (see Table S1 for further details). Hand and foot information was not uniformly represented in these ROIs. Although all ROIs significantly encoded hand information (one-sample t test, $t(22) = 2.10$, uncorrected $P = 0.024$, Cohen's $d = 0.44$ in Tha/PHG; $t(22) > 2.80$, Bonferroni-corrected $ps < 0.030$, Cohen's $d > 0.58$ in other regions), with SMA/PMd and pIPS encoding more hand information than foot information (paired t test, $t(22) > 2.11$,

Downloaded from academic.oup.com/cercor/article/33/11/6862/6995384 by guest on 23 September 2026

uncorrected $ps < 0.046$, Cohen's $d > 0.44$), foot information was observed in only SMA/PMd, vmPFC/IFG and Tha/PHG ($t(22) > 2.79$, Bonferroni-corrected $ps < 0.030$, Cohen's $d > 0.58$; $t(22) < 1.41$, uncorrected $ps > 0.086$ in other regions).

We then tested verb effector × HDBR training interaction in each region. Only the right Tha/PHG cluster yielded a significant interaction effect ($F(1,22) = 11.62$, Bonferroni-corrected $P = 0.018$, partial $\eta^2 = 0.35$ in Tha/PHG; $F(1,22) < 0.77$, uncorrected $ps > 0.390$ in other areas). The interaction in the Tha/PHG was driven by the significantly decreased foot verb information representation after HDBR training ($t(22) = 5.38$, $P < 0.001$, Cohen's $d = 1.12$) and the absence of hand verb information change ($t(22) = 0.04$, $P = 0.969$). For regions with nonsignificant interactions, we further performed Bayesian ANOVAs to examine the likelihood of a genuine absence of effects. The Bayesian factor yielded moderate evidence for H_0 (no interaction effect) in the left SMA/PMd, left pIPS and left LPTC (all $BF_{incl} < 0.33$), and anecdotal evidence for H_0 in the vmPFC/left IFG ($BF_{incl} = 0.35$) and right ROL/STG ($BF_{incl} = 0.49$) (see Table S2 and Fig. 2a). That is, although some effector-specific verb semantic regions (especially the left SMA/PMd, left pIPS and left LPTC) were independent from short-term motor experience deprivation, the right Tha/PHG's encoding of verb semantics was altered in an effector-content-specific manner.

Left ATL

We then examined whether the general semantic area, left ATL, was modulated by short-term motor experience (Fig. 2b, left panel). This region significantly encoded both hand and foot information in pre-HDBR (one-sample t test, $t(22) = 2.63$, one-tailed $P = 0.008$, Cohen's $d = 0.55$ for hand information; $t(22) = 3.72$, one-tailed $P < 0.001$, Cohen's $d = 0.78$ for foot information). It also showed a significant effector × HDBR training interaction effect ($F(1,22) = 5.57$, $P = 0.028$, partial $\eta^2 = 0.20$), which was driven by the significantly decreased foot information after HDBR training ($t(22) = 3.72$, two-tailed $P = 0.001$, Cohen's $d = 0.78$) together with non-significant hand verb information change ($t(22) = -0.32$, two-tailed $P = 0.753$).

M1/S1 motor execution areas

The M1/S1 hand and foot motor execution areas (Fig. 2c, left panel) were functionally localised by contrasting foot with hand motor execution (and vice versa) in a pre-HDBR motor execution-imagery task (thresholded at voxel-level FWE-corrected $P < 0.05$; see Supplementary Materials for details). For the activation of action verbs in these areas, in the pre-HDBR data, although our univariate analyses largely replicated previous findings that effector-specific action verbs activated corresponding effector-specific motor areas (Fig. S1), we did not observe significant encoding of effector information in multivoxel pattern analyses (one-sample t test, hand information in hand area, $t(22) = 1.36$, one-tailed $P = 0.094$; foot information in foot area, $t(22) = 1.29$, one-tailed $P = 0.106$). Repeated-measures ANOVA only revealed a nonsignificant trend of ROI (hand, foot area) × verb effector (hand, foot verbs) interaction ($F(1,22) = 2.91$, $P = 0.102$). The effector × HDBR training interaction did not approach statistical significance in either foot or hand areas ($F(1,22) < 0.30$, $ps > 0.587$), which was further confirmed by Bayesian ANOVAs ($BF_{incl} = 0.29$, moderate evidence for H_0 in foot region; $BF_{incl} = 0.36$, anecdotal evidence for H_0 in hand region). Together, these results indicated that activation patterns of M1/S1 motor areas did not significantly encode effector information and were not significantly modulated by HDBR experience.

Whole-brain results of verb effector × HDBR training interactions

We additionally performed a whole-brain information-based searchlight analysis (Kriegeskorte et al. 2006) to uncover other brain regions potentially showing the verb effector × HDBR training interaction effects. Significant interaction effects (F test, thresholded at voxel-level $P < 0.001$, cluster-level FWE-corrected $P < 0.05$) were observed in two clusters (Fig. 3a, left panel): a subcortical cluster encompassing the ventromedial thalamus, subthalamic nucleus (STN), substantia nigra and hypothalamus (peak MNI coordinates 12, −12, −3, peak $F(1,22) = 50.64$, 94 voxels), and an dorsal anterior temporal cluster, extending to the left anterior insula, and left IFG (peak MNI coordinates −42, 15, −15, peak $F(1,22) = 32.30$, 91 voxels). As the anterior temporal cluster extended to the insular-frontal regions, we further performed small volume correction within the left ATL mask we used in the ROI analyses and found that the anterior temporal voxels survived the correction (23 voxels, voxel-level $P < 0.001$, cluster-level FWE-corrected $P = 0.023$), which was consistent with the ROI-level ATL results. In both regions, the interaction was in the direction of decreased foot verb information ($t(22) > 4.46$, $ps < 0.001$, Cohen's $d > 0.93$) and non-significant change of hand information ($t(22) < -0.39$, $ps > 0.202$) after HDBR training. We presented the group-averaged neural RSM results of the two regions in the pre- and post-HDBR data in Fig. 3a (right panel) for illustration purpose. The neural RSMs showed that the similarity for foot verbs (between the split-half activity patterns of same or different words) were all significantly above zero prior to HDBR, and largely became not significantly different from zero after HDBR, indicating that, indeed, the foot verb representations in these regions were diminished by HDBR.

Relationship across regions showing verb effector × HDBR training interactions: Connectivity results

The whole-brain searchlight analyses and the ROI analyses above converge on two regions, the right subcortical regions and the left anterior temporal cluster, whose verb semantic representation was modulated by short-term motor deprivation in an effector-specific manner, such that more salient lower limb constraints led to the attenuation of neural representations of words referring to foot actions (to kick, to stomp), more so than to hand actions (to scratch, to pinch). To understand whether the two regions' information modulation was related and the potential neural origins of such changes, we performed the following resting-state connectivity analyses (rsFC).

Given the importance of reliability analyses for rsFC, resting-state neuroimaging scans in an independent larger sample ($n = 144$, all right-handers), whose test-retest reliability has been established (Lin et al., 2015b), were used for the rsFC analyses. Intriguingly, these two regions were not functionally connected at rest (Fisher-z-transformed FC strength, $M \pm SD = -0.02 \pm 0.24$, $t(143) = -0.94$, one-tailed $P = 0.827$), whereas each showed rsFC with widely distributed regions (Fig. 3b; thresholded at voxel-level FWE-corrected, one-tailed $P < 0.05$, cluster size > 50 voxels). The subcortical cluster was intrinsically connected with subcortical areas encompassing the cerebella, brainstem, midbrain and posterior cingulate cortex; the anterior temporal cluster was intrinsically connected with areas including bilateral temporal-frontal regions encompassing the inferior/middle frontal gyri and middle/superior temporal gyri. Importantly, the two seed clusters showed overlaps in rsFC patterns in the SMA, basal ganglia, insula,

Downloaded from academic.oup.com/cercor/article/33/11/6862/6995384 by guest on 23 September 2026

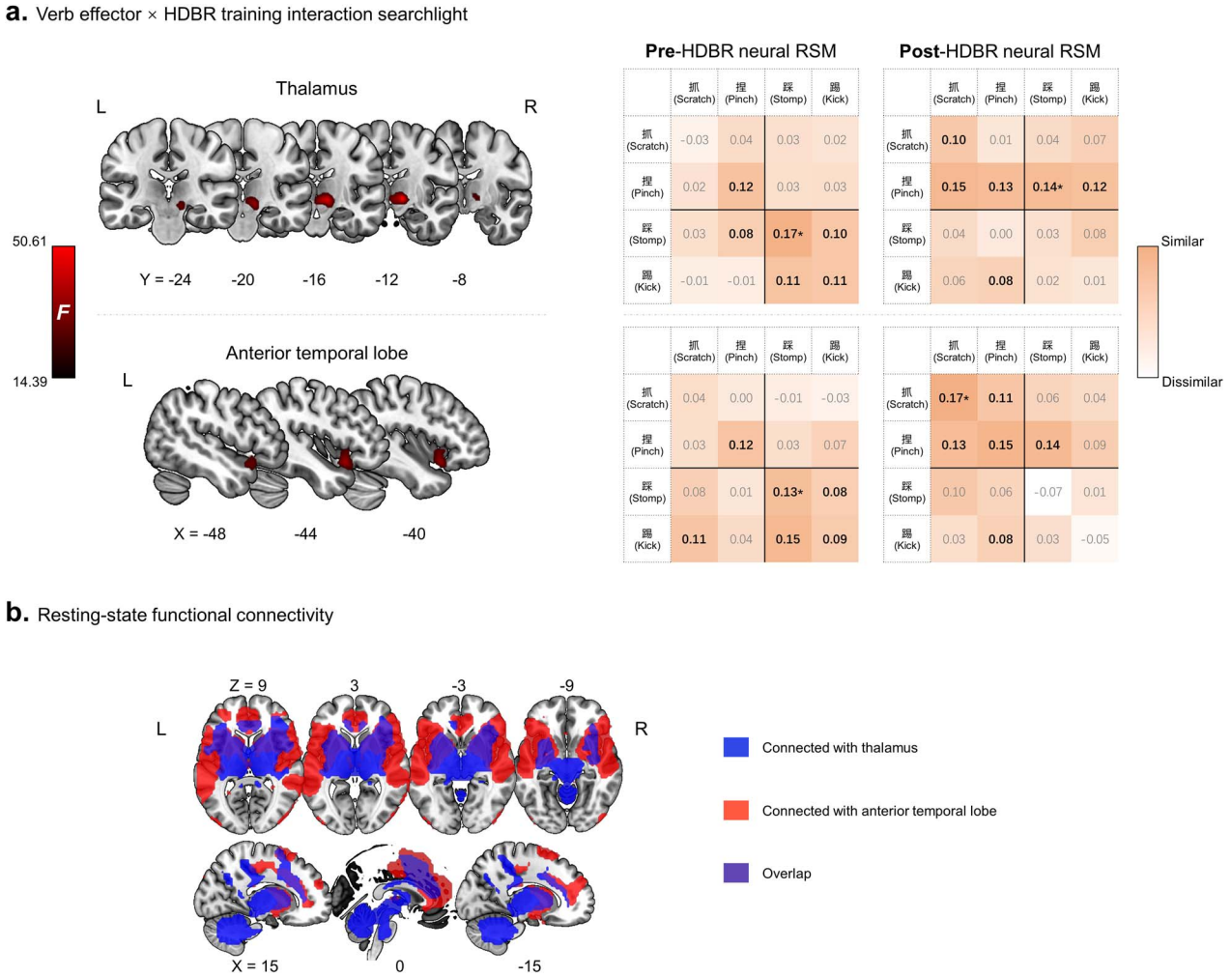

Fig. 3. Two regions showing verb effector (hand, foot) × HDBR training (pre-HDBR, post-HDBR) interaction effects in the whole-brain searchlight analysis. (a) The left panel illustrates the anatomical locations of two clusters showing verb effector (hand, foot) × HDBR training (pre-HDBR, post-HDBR) interaction effects in the whole-brain searchlight analysis (thresholded at voxel-level $P < 0.001$, cluster-level FWE-corrected $P < 0.05$). Right panel: the group-averaged neural representation similarity matrix (RSM) shown in each region at each phase (pre- and post-HDBR), respectively. Numbers in bold fonts indicate that the correlations between neural activity patterns (Fisher-z-transformed Pearson's r values) were significantly above zero across subjects, uncorrected $P < 0.05$; asterisks indicate Bonferroni-corrected $P < 0.05$ (number of corrections = 16). (b) rsFC maps of the two clusters (the thalamus cluster, blue; the anterior temporal cluster, red) and their overlap (purple) in an independent group of young healthy subjects ($n = 144$). The maps were thresholded at voxel-level FWE-corrected $P < 0.05$, cluster size > 50 voxels. L: left; R: right.

anterior cingulate cortex and thalamus (Fig. 3b) that have been consistently implicated in motor processing (see Discussion).

Discussion

In the current study, we tested the role of sensorimotor experience on dynamically shaping the neural representation of common verb semantics using HDBR—a spaceflight analog that alters (deprives) the subjects' lower limb sensorimotor experience most strongly relative to other actions. By collecting fMRI BOLD responses to verbs of lower- and upper-limb actions and comparing their multivoxel activation patterns before and after HDBR, we found that a 15-day motor experience deprivation modulated the verb neural representation in an effector-specific manner in a subcortical cluster and a left anterior temporal cluster (in both ROI and whole-brain searchlight analyses), but not in other regions showing verb effector-specific-content representation (e.g. the left LPTC, SMA/PMd) or in M1/S1 areas. Resting-state connectivity analysis revealed that the subcortical and the dorsal ATL clusters shared common intrinsic connectivity patterns. Taken together, our results highlight the brain regions (the subcortical and the ATL cluster) whose semantic representations are sensitive to short-term motor experience modulation, along with other brain regions (motor execution and effector-specific verb semantic areas) that are left unchanged.

In the pre-HDBR fMRI data, our univariate analyses replicated the effector-specific somatotopic organisation for action verbs in the M1/S1 (Fig. S1) and our multivoxel analyses found verb semantic representation in clusters located in the left LPTC, IFG and association sensorimotor cortices (PMd/SMA, pIPS), which are largely consistent with previous studies and support the validity and sensitivity of our experimental design. We focused on discussing the positive and negative effects of the temporary experience modulation below.

Effector-specific modulation by HDBR of action-related regions in action verb understanding

The subcortical regions we observed in the functional localisation of effector information and in the whole-brain searchlight

Downloaded from academic.oup.com/cercor/article/33/11/6862/6995384 by guest on 23 September 2026

analyses for HDBR-induced effector-specific modulation converged well. This cluster encompassed the STN, ventromedial thalamus (Tha), substantia nigra, hypothalamus and the surrounding subcortical structures. This cluster is part of the subcortical subregions of the motor system (Obeso et al. 2008). STN and Tha show somatotopic organisation, i.e. effector-specific arrangement, based on neural activation recorded during surgery (Rodriguez-Oroz et al. 2001; Theodosopoulos et al. 2003). The cluster is activated in motor execution tasks according to a recent meta-analysis on fMRI studies (Hardwick et al. 2018), and also overlaps with the lesion sites in PD, where patients exhibit motor deficits such as reduced movements, tremor during rest and postural instability (Halliday 2009; Rodriguez-Oroz et al. 2009). The involvement of this region in action semantic knowledge has been hinted by action verb impairment in PD patients. These patients show disproportionate impairment in comprehending action verbs (e.g. "to grasp") than abstract verbs (e.g. "to depend"; Fernandino et al. 2013a), in comprehending sentences with action verbs relative to sentences with abstract verbs (Fernandino et al. 2013b), and in verb generation relative to noun generation (Patrice et al. 2003; Rodríguez-Ferreiro et al. 2009). Here applying multivoxel pattern correlation analysis, we provide the first piece of neuroimaging evidence that this region significantly encodes action knowledge representation, which is dynamically coupled with the corresponding motor experience and/or gravity change in an effector-specific manner.

For other action-related regions, our pre-HDBR searchlight analyses of effector information successfully identified several regions that are consistent with the literature (e.g. Wurm and Caramazza 2021), such as the left LPTC and association sensorimotor cortices (PMd, SMA, pIPS). They did not show any changes in terms of foot action word neural representation after 15-day HDBR, with Bayesian ANOVA yielding moderate evidence for H_0, whereas our results were inconclusive about the left IFG. The absence of motor experience modulation in these regions was unlikely to be due to false-negatives, as supported by Bayesian statistics, and effector-specific changes were observed in other brain regions (the temporal and the subcortical clusters). The immunity to short-term experience deprivation in LPTC and pIPS is in line with the findings showing that the action representations in these regions are abstracted away from specific motor programs (open a bottle and open a box, for IPS and lateral occipitotemporal cortex, slightly posterior to LPTC) and/or sensory modalities (conveyed through visual input or verbal input, LPTC; Wurm and Lingnau 2015; Wurm et al. 2016; Wurm and Caramazza 2019). The absence of signal pattern change modulation by HDBR in M1/S1 and SMA/PMd is not consistent with previous studies that reported changes (in different directions) for M1/S1 and PMd activation strength during action language understanding induced by motor experience enrichment (e.g. ice hockey playing in Beilock et al. 2008 and Lyons et al. 2010). These previous studies tested the effects of complex experience acquisition, and it is possible that neural representation there was only modulated by experience enrichment and not by short-term deprivation and/or attributable to effects beyond specific motor experience. Another explanation for the lack of motor experience deprivation in these regions is that they exhibited relatively lower sensitivity to foot verbs compared with hand verbs, especially in SMA/PMd and pIPS. In contrast, the subcortical cluster discussed above significantly encoded foot information before HDBR, which was numerically higher than hand information. It is thus possible that neuroplasticity respects the original neural organisation principle, with lower-limb motor deprivation specifically modulating regions encoding lower-limb action verbs.

Anterior temporal region showing effector-specific modulation by HDBR in action verb understanding

In our study, ROI-level analyses showed that the left ATL exhibited HDBR's effector-specific modulation and the whole-brain searchlight revealed similar effects in the dorsal portion of the left ATL. The ATL is one of the critical regions for semantic representation that has been extensively discussed (Lambon Ralph et al. 2017; Xu et al. 2017). Before HDBR, we observed significant encoding of hand and foot information in this region, which is consistent with its role in general semantic representation. The ATL is comprised of fine-grained functional subdivisions (Fan et al. 2014; Wang et al. 2019; Hung et al. 2020). The results in the left dorsal ATL cluster observed in the whole-brain searchlight analysis were a little puzzling. The left dorsal ATL is consistently engaged in abstract semantic representation (Binder et al. 2009; Wang et al. 2010; Striem-Amit et al. 2018; Wang et al. 2019), which is fully abstracted away from specific sensorimotor experiences, and assumed to represent knowledge derived from language (Wang et al. 2020, see Bi 2021 for review; see also Lambon Ralph et al. 2017 for similar positions). It was thus not one of the regions hypothesised to change with sensorimotor experience variations. On the other hand, resting-state connectivity analyses showed that although not directly connected with the subcortical cluster, it is intrinsically connected with widely distributed regions, especially the ones commonly connected with the subcortical cluster showing modulation of HDBR: the medial frontal and subcortical motor-control areas—SMA, basal ganglia, insula, anterior cingulate cortex and thalamus. Connected via the cortico-basal ganglia-thalamo-cortical loop, these regions have been reported to involve in motor execution, motor imagery, motor sequence learning and action observation (Caspers et al. 2010; Hardwick et al. 2018). A recent study revealed that learning action verbs with novel motor actions leads to rapid neuroanatomical changes in the left ATL (including the dorsal part), an effect dependent on whether TMS was exerted on the left M1 (Vukovic et al. 2021). One possibility about the pattern of HDBR modulation in the left (dorsal) ATL may be arising not from its direct involvement in sensorimotor experiences, but rather from its tight connections with different semantic regions and/or networks (Xu et al. 2016; Lambon Ralph et al. 2017; Xu et al. 2017), including the sensorimotor systems, and/or the language experience changes that are associated with the sensorimotor experience alteration. Verbs relating to lower limbs may be used less frequently than hand verbs during the 15-day HDBR, which we did not monitor in our study. Future studies are warranted to test such speculations and to further understand the mechanisms underlying the dynamic semantic representations in this region.

Conclusion

We found that 15-day HDBR mimicking of microgravity significantly weakened the neural representation of action verbs in subcortical motor regions and the left anterior temporal region in an effector-specific manner. That is, the brain's representations for "to stomp" and "to kick" in these two regions were reduced, but there was no such change for "to scratch" or "to pinch" after the bed rest. The neural representations of action semantics in sensorimotor areas (M1/S1), and the widely distributed effector-specific verb semantic regions (left LPTC, left SMA/PMd and left

Downloaded from academic.oup.com/cercor/article/33/11/6862/6995384 by guest on 23 September 2026

pIPS) were not affected. These sensorimotor-experience-induced and sensorimotor-experience-independent patterns of verb neural representation highlight the multidimensional and dynamic nature of neural semantic representation in general. These findings also highlight the broad influence of microgravity (hence gravity) on knowledge and cognition.

Acknowledgments

We thank Professor Yong He for generously sharing the resting-state data.

Supplementary material

Supplementary material is available at *Cerebral Cortex* online.

Funding

This work was supported by the STI2030-Major Project (2021ZD0204100 (2021ZD0204104) to Y.B., 2021ZD0202600 (2021ZD0202601) to K.W.); the Space Medical Experiment Project of China Manned Space Program (HYZHXM03002 to K.W.); the National Natural Science Foundation of China (31925020, 82021004 to Y.B., 62061136001, 32071047, 31871102 to K.W., 32171052 to X.W.); the Changjiang Scholar Professorship Award (T2016031 to Y.B.). The funders had no role in the conceptualisation, design, data collection, analysis, decision to publish or preparation of the manuscript.
Conflicts of interest statement: None declared.

Author contributions

Ziyi Xiong: Formal Analysis, Investigation, Methodology, Validation, Visualization, Writing - original draft, Writing - review & editing. **Yu Tian**: Data curation, Methodology, Resources, Writing - review & editing. **Xiaosha Wang**: Conceptualization, Formal Analysis, Funding acquisition, Investigation, Methodology, Resources, Supervision, Validation, Writing - original draft, Writing - review & editing. **Kunlin Wei**: Conceptualization, Funding acquisition, Project administration, Resources, Supervision, Writing - review & editing. **Yanchao Bi**: Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Writing - original draft, Writing - review & editing.

Data availability

All data reported in this study have been made publicly available via Open Science Framework and can be accessed at https://osf.io/cjnxs/.

References

Bedny M, Caramazza A, Grossman E, Pascual-Leone A, Saxe R. Concepts are more than percepts: the case of action verbs. *J Neurosci*. 2008:28(44):11347–11353.

Beilock SL, Lyons IM, Mattarella-Micke A, Nusbaum HC, Small SL. Sports experience changes the neural processing of action language. *Proc Natl Acad Sci*. 2008:105(36):13269–13273.

Bi Y. Dual coding of knowledge in the human brain. *Trends Cogn Sci*. 2021:25(10):883–895.

Binder JR, Desai RH, Graves WW, Conant LL. Where is the semantic system? A critical review and meta-analysis of 120 functional neuroimaging studies. *Cereb Cortex*. 2009:19(12):2767–2796.

Cai Q, Brysbaert M. SUBTLEX-CH: Chinese word and character frequencies based on film subtitles. *PLoS One*. 2010:5(6):e10729.

Caramazza A, Anzellotti S, Strnad L, Lingnau A. Embodied cognition and mirror neurons: a critical assessment. *Annu Rev Neurosci*. 2014:37(1):1–15.

Caspers S, Zilles K, Laird AR, Eickhoff SB. ALE meta-analysis of action observation and imitation in the human brain. *NeuroImage*. 2010:50(3):1148–1167.

Coutanche MN, Thompson-Schill SL. Creating concepts from converging features in human cortex. *Cereb Cortex*. 2015:25(9):2584–2593.

Fan L, Wang J, Zhang Y, Han W, Yu C, Jiang T. Connectivity-based parcellation of the human temporal pole using diffusion tensor imaging. *Cereb Cortex*. 2014:24(12):3365–3378.

Fernandino L, Conant LL, Binder JR, Blindauer K, Hiner B, Spangler K, Desai RH. Parkinson's disease disrupts both automatic and controlled processing of action verbs. *Brain Lang*. 2013a:127(1):65–74.

Fernandino L, Conant LL, Binder JR, Blindauer K, Hiner B, Spangler K, Desai RH. Where is the action? Action sentence processing in Parkinson's disease. *Neuropsychologia*. 2013b:51(8):1510–1517.

Halliday GM. Thalamic changes in Parkinson's disease. *Parkinsonism Relat Disord*. 2009:15:S152–S155.

Hardwick RM, Caspers S, Eickhoff SB, Swinnen SP. Neural correlates of action: comparing meta-analyses of imagery, observation, and execution. *Neurosci Biobehav Rev*. 2018:94:31–44.

Hauk O, Johnsrude I, Pulvermüller F. Somatotopic representation of action words in human motor and premotor cortex. *Neuron*. 2004:41(2):301–307.

Haushofer J, Livingstone MS, Kanwisher N. Multivariate patterns in object-selective cortex dissociate perceptual and physical shape similarity. *PLoS Biol*. 2008:6(7):e187.

Haxby JV, Gobbini MI, Furey ML, Ishai A, Schouten JL, Pietrini P. Distributed and overlapping representations of faces and objects in ventral temporal cortex. *Science*. 2001:293(5539):2425–2430.

Hung J, Wang X, Wang X, Bi Y. Functional subdivisions in the anterior temporal lobes: a large scale meta-analytic investigation. *Neurosci Biobehav Rev*. 2020:115:134–145.

JASP Team. *JASP (version 0.16.2)[computer software]*. New York, NY: Pergamon Press; 2022

Kontra C, Lyons DJ, Fischer SM, Beilock SL. Physical experience enhances science learning. *Psychol Sci*. 2015:26(6):737–749.

Koppelmans V, Bloomberg JJ, De Dios YE, Wood SJ, Reuter-Lorenz PA, Kofman IS, Riascos R, Mulavara AP, Seidler RD. Brain plasticity and sensorimotor deterioration as a function of 70 days head down tilt bed rest. *PLoS One*. 2017:12(8):e0182236.

Kriegeskorte N, Goebel R, Bandettini P. Information-based functional brain mapping. *Proc Natl Acad Sci*. 2006:103(10):3863–3868.

Lambon Ralph MA, Jefferies E, Patterson K, Rogers TT. The neural and computational bases of semantic cognition. *Nat Rev Neurosci*. 2017:18(1):42–55.

Lin N, Wang X, Zhao Y, Liu Y, Li X, Bi Y. Premotor cortex activation elicited during word comprehension relies on access of specific action concepts. *J Cogn Neurosci*. 2015a:27(10):2051–2062.

Lin Q, Dai Z, Xia M, Han Z, Huang R, Gong G, Liu C, Bi Y, He Y. A connectivity-based test-retest dataset of multi-modal magnetic resonance imaging in young healthy adults. *Sci Data*. 2015b:2(1):1–10.

Lyons IM, Mattarella-Micke A, Cieslak M, Nusbaum HC, Small SL, Beilock SL. The role of personal experience in the neural

Downloaded from academic.oup.com/cercor/article/33/11/6862/6995384 by guest on 23 September 2026

processing of action-related language. *Brain Lang*. 2010:112(3): 214–222.

Mumford JA, Davis T, Poldrack RA. The impact of study design on pattern estimation for single-trial multivariate pattern analysis. *NeuroImage*. 2014:103:130–138.

Obeso JA, Rodríguez-Oroz MC, Benitez-Temino B, Blesa FJ, Guridi J, Marin C, Rodriguez M. Functional organization of the basal ganglia: therapeutic implications for Parkinson's disease. *Mov Disord*. 2008:23(S3):S548–S559.

Patrice P, Olivier R, Jean-Franois D, Pierre C, Jean-Luc, & Nespoulous. Deficit of verb generation in nondemented patients with Parkinson's disease. *Mov Disord*. 2003:18(2):150–156.

Poldrack RA. Can cognitive processes be inferred from neuroimaging data? *Trends Cogn Sci*. 2006:10(2):59–63.

Pulvermüller F. Brain mechanisms linking language and action. *Nat Rev Neurosci*. 2005:6(7):576–582.

Repetto C, Colombo B, Cipresso P, Riva G. The effects of rTMS over the primary motor cortex: the link between action and language. *Neuropsychologia*. 2013:51(1):8–13.

Rodríguez-Ferreiro J, Menéndez M, Ribacoba R, Cuetos F. Action naming is impaired in Parkinson disease patients. *Neuropsychologia*. 2009:47(14):3271–3274.

Rodriguez-Oroz MC, Rodriguez M, Guridi J, Mewes K, Chockkman V, Vitek J, DeLong MR, Obeso JA. The subthalamic nucleus in Parkinson's disease: somatotopic organization and physiological characteristics. *Brain*. 2001:124(9):1777–1790.

Rodriguez-Oroz MC, Jahanshahi M, Krack P, Litvan I, Macias R, Bezard E, Obeso JA. Initial clinical manifestations of Parkinson's disease: features and pathophysiological mechanisms. *Lancet Neurol*. 2009:8(12):1128–1139.

Song X-W, Dong Z-Y, Long X-Y, Li S-F, Zuo X-N, Zhu C-Z, He Y, Yan C-G, Zang Y-F. REST: a toolkit for resting-state functional magnetic resonance imaging data processing. *PLoS One*. 2011:6(9):e25031.

Striem-Amit E, Wang X, Bi Y, Caramazza A. Neural representation of visual concepts in people born blind. *Nat Commun*. 2018:9(1):1–12.

Tettamanti M, Buccino G, Saccuman MC, Gallese V, Danna M, Scifo P, Fazio F, Rizzolatti G, Cappa SF, Perani D. Listening to action-related sentences activates fronto-parietal motor circuits. *J Cogn Neurosci*. 2005:17(2):273–281.

Theodosopoulos PV, Marks WJ Jr, Christine C, Starr PA. Locations of movement-related cells in the human subthalamic nucleus in Parkinson's disease. *Mov Disord*. 2003:18(7):791–798.

van den Bergh D, Van Doorn J, Marsman M, Draws T, Van Kesteren E-J, Derks K, Dablander F, Gronau QF, Kucharský Š, Gupta ARKN. A tutorial on conducting and interpreting a Bayesian ANOVA in JASP. *Annee Psychol*. 2020:120(1):73–96.

Vukovic N, Feurra M, Shpektor A, Myachykov A, Shtyrov Y. Primary motor cortex functionally contributes to language comprehension: an online rTMS study. *Neuropsychologia*. 2017:96:222–229.

Vukovic N, Hansen B, Lund TE, Jespersen S, Shtyrov Y. Rapid microstructural plasticity in the cortical semantic network following a short language learning session. *PLoS Biol*. 2021:19(6): e3001290.

Wang J, Conder JA, Blitzer DN, Shinkareva SV. Neural representation of abstract and concrete concepts: a meta-analysis of neuroimaging studies. *Hum Brain Mapp*. 2010:31(10):1459–1468.

Wang X, Zhuang T, Shen J, Bi Y. Disentangling representations of shape and action components in the tool network. *Neuropsychologia*. 2018:117:199–210.

Wang X, Wang B, Bi Y. Close yet independent: dissociation of social from valence and abstract semantic dimensions in the left anterior temporal lobe. *Hum Brain Mapp*. 2019:40(16): 4759–4776.

Wang X, Men W, Gao J, Caramazza A, Bi Y. Two forms of knowledge representations in the human brain. *Neuron*. 2020:107(2):383–393 e385.

Wang Y, Zhang X, Wang C, Huang W, Xu Q, Liu D, Zhou W, Chen S, Jiang Y. Modulation of biological motion perception in humans by gravity. *Nat Commun*. 2022:13(1):1–10.

Warburton E, Wise RJ, Price CJ, Weiller C, Hadar U, Ramsay S, Frackowiak RS. Noun and verb retrieval by normal subjects studies with PET. *Brain*. 1996:119(1):159–179.

Willems RM, Hagoort P, Casasanto D. Body-specific representations of action verbs: neural evidence from right-and left-handers. *Psychol Sci*. 2010:21(1):67–74.

Willems RM, Labruna L, D'Esposito M, Ivry R, Casasanto D. A functional role for the motor system in language understanding: evidence from theta-burst transcranial magnetic stimulation. *Psychol Sci*. 2011:22(7):849–854.

Wurm MF, Caramazza A. Distinct roles of temporal and frontoparietal cortex in representing actions across vision and language. *Nat Commun*. 2019:10(1):1–10.

Wurm MF, Caramazza A. Two 'what'pathways for action and object recognition. *Trends Cogn Sci*. 2021:26(2):103–116.

Wurm MF, Lingnau A. Decoding actions at different levels of abstraction. *J Neurosci*. 2015:35(20):7727–7735.

Wurm MF, Ariani G, Greenlee MW, Lingnau A. Decoding concrete and abstract action representations during explicit and implicit conceptual processing. *Cereb Cortex*. 2016:26(8): 3390–3401.

Xia M, Wang J, He Y. BrainNet Viewer: a network visualization tool for human brain connectomics. *PLoS One*. 2013:8(7):e68910.

Xu Y, Lin Q, Han Z, He Y, Bi Y. Intrinsic functional network architecture of human semantic processing: modules and hubs. *NeuroImage*. 2016:132:542–555.

Xu Y, He Y, Bi Y. A tri-network model of human semantic processing. *Front Psychol*. 2017:8:1538.

Xu Y, Wang X, Wang X, Men W, Gao J-H, Bi Y. Doctor, teacher, and stethoscope: neural representation of different types of semantic relations. *J Neurosci*. 2018:38(13):3303–3317.

Yang H, Lin Q, Han Z, Li H, Song L, Chen L, He Y, Bi Y. Dissociable intrinsic functional networks support noun-object and verb-action processing. *Brain Lang*. 2017:175: 29–41.

Yu X, Law SP, Han Z, Zhu C, Bi Y. Dissociative neural correlates of semantic processing of nouns and verbs in Chinese—a language with minimal inflectional morphology. *NeuroImage*. 2011:58(3): 912–922.

Yuan P, Koppelmans V, Reuter-Lorenz P, De Dios Y, Gadd N, Wood S, Riascos R, Kofman I, Bloomberg J, Mulavara A. Vestibular brain changes within 70 days of head down bed rest. *Hum Brain Mapp*. 2018:39(7):2753–2763.

Downloaded from academic.oup.com/cercor/article/33/11/6862/6995384 by guest on 23 September 2026