



# Open-ended movements structure sensorimotor information in early human development

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Human behaviors, with whole-body coordination, involve large-scale sensorimotor interaction. Spontaneous bodily movements in the early developmental stage potentially lead toward acquisition of such coordinated behavior. These movements presumably contribute to the structuration of sensorimotor interaction, providing specific regularities in bidirectional information among muscle activities and proprioception. Whether and how spontaneous movements, despite being task-free, structure and organize sensorimotor interactions in the entire body during early development remain unknown. Herein, to address these issues, we gained insights into the structuration process of the sensorimotor interaction in neonates and 3-mo-old infants. By combining detailed motion capture and musculoskeletal simulation, sensorimotor information flows among muscle activities and proprioception throughout the body were obtained. Subsequently, we extracted spatial modules and temporal state in sensorimotor information flows. Our approach demonstrated that early spontaneous movements elicited body-dependent sensorimotor modules, revealing age-related changes in them, depending on the combination or direction. The sensorimotor interactions also displayed temporal non-random fluctuations analogous to those seen in spontaneous activities in the cerebral cortex and spinal cord. Furthermore, we found recurring state sequence patterns across multiple participants, characterized by a substantial increase in infants compared to the patterns in neonates. Therefore, early spontaneous movements induce the spatiotemporal structuration in sensorimotor interactions and subsequent developmental changes. These results implicated that early open-ended movements, emerging from a certain neural substrate, regulate the sensorimotor interactions through embodiment and contribute to subsequent coordinated behaviors. Our findings also provide a conceptual linkage between early spontaneous movements and spontaneous neuronal activity in terms of spatiotemporal characteristics.

dynamics | primitive | synergy | network | curiosity

In the early developmental stage, spontaneous bodily movements presumably play essential roles in sensorimotor development (1–3). These early movements, although they are not goal-directed, provide specific regularities in bidirectional information among muscle activities and proprioception (i.e., sensorimotor interactions). Accumulated physiological knowledge from animal experiments suggests that bodily movement regulates sensory inputs, resulting in the modulation of functional and anatomical neuronal connectivity. Subsequently, this could recursively contribute as a self-organizing process to the developmental changes in motor control and behavior (4–6). The establishment of coordinated behavior can be accounted for by unsupervised learning in spontaneous movements (6), characterized by the spatiotemporal organization of the activity of motor and sensory neurons in the spinal cord (7). Somatosensory information processing in the central nervous system (CNS) is involved in spontaneous movements (8, 9), in which a disturbance causes abnormal sensorimotor circuits whether by neural inactivation or environmental constraints (10, 11).

Before the emergence of intentional motor control, the human fetus and neonate exhibit unique and complex spontaneous whole-body movements, which some have considered key to understanding human nature for more than a century (12, 13). Observational studies on early spontaneous movements have reported age-related changes in kinematic patterns (14, 15), frequency of limb movements (16), intra- and inter-limb coordination (17), property of muscle activities (18–21), or functional coupling (22, 23), thereby suggesting the role of neuronal maturation of the sensorimotor system behind these changes (24). Clinical studies provide evidence for the presence of atypical movements as a predictive biomarker of developmental disorders, particularly cerebral palsy, thus indicating its functional representativeness with regard to the CNS (24–26). Spontaneous bodily movements are supposedly induced by spontaneous neuronal activities, which are a general feature of the developing neuronal system (5) and pattern generators in the spinal cord, brainstem, or motor cortex (9).

## Significance

It is postulated that the various human behaviors, consisting structured sensorimotor interactions, are established based on experiences from the early developmental stage. From this perspective, spontaneous whole-body movements, which neonates and infants specifically exhibit without an explicit purpose like “sensorimotor wandering,” could contribute to the structuration of the sensorimotor interactions later observed in task-specific movements, such as walking or reaching. In this research, we identified both spatial and temporal structures in muscular sensorimotor interactions under spontaneous movements and their developmental changes during early infancy. These findings highlight the contribution of early open-ended movements to the self-organized structuring of sensorimotor interactions. Moreover, they further provide conceptual insight that links early whole-body movements to spontaneous neuronal activity maturing in an autonomous fashion.

The authors declare no competing interest.

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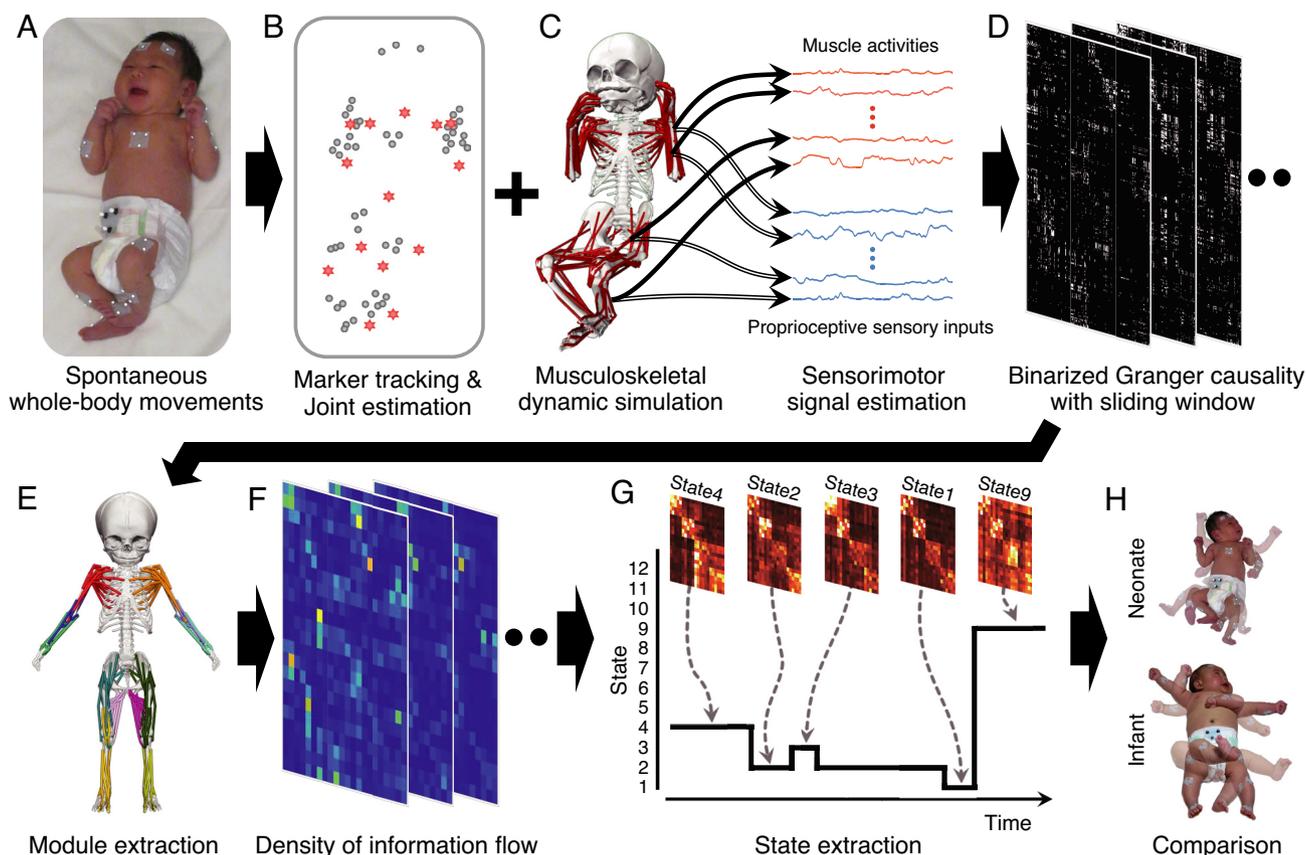
Synthetically, considering developmental science, neuroscience, and robotics, human behavioral and cognitive development presumably emerges from the brain–body–behavior networks by expanding the self-organizing process in the nervous system (27–30). Accordingly, dynamic mutual interactions across timescales between the brain, body, and environment based on sensorimotor interactions could contribute to developmental changes in the functional and structural brain networks. This in turn could modulate subsequent behavioral patterns across disparate domains (27).

Despite fairly convincing evidence for the prominent role of spontaneous movements in sensorimotor development, there is limited knowledge of the structuring and dynamics consisting of motor outputs and various sensory inputs during early human infancy. Sensorimotor interactions during early spontaneous movements are concomitant with incessant motor activities and sensory feedback involving multiple muscles throughout the whole body. Nevertheless, studies of infantile movements have principally focused on a limited number of partial characteristics such as motion trajectory. Moreover, only one side of the factors, i.e., motor outputs, has been focused on, for mostly steady state. To the best of our knowledge, researchers have not investigated the dynamic and multiple motor activities and sensory feedback owing to insufficient available measurement. Thus, whether and how dynamic and multiple sensorimotor interactions, which presumably form the basis of later motor behaviors, are structured through early whole-body spontaneous movements remains unknown.

Herein, we quantified sensorimotor interaction among muscle activities and proprioceptive inputs estimated by combining detailed motion capture and musculoskeletal simulation in human neonates and 3-mo-old infants. The aim of this study was to delineate the spatiotemporal patterns of sensorimotor interactions during spontaneous whole-body movements in the early developmental stage to gain insights into the structuration process of the sensorimotor system. We hypothesized that early spontaneous whole-body movements self-organize spatial and temporal structures in sensorimotor interactions, which potentially lead toward the acquisition of coordinated behavior (*SI Appendix, Fig. S1*).

## Results

**Whole-Body Sensorimotor Interactions during Spontaneous Movements.** First, we captured whole-body motion data during spontaneous movements for 60 s without external stimulation from 12 healthy neonates aged <10 d (5 boys, 7 girls; weight:  $2,877 \pm 364$  g; height:  $48 \pm 2.4$  cm) and ten 3-mo-old infants (6 boys, 4 girls; weight:  $6,152 \pm 962$  g; height:  $60 \pm 3.9$  cm) with a three-dimensional motion capture system (Fig. 1 *A* and *B*). We obtained a total of 12 joint movements (right and left shoulder, elbow, wrist, hip, knee, and ankle) with 26 degrees of freedom via inverse kinematics. No significant difference existed in joint angle velocity between the neonate and infant groups. Moreover, to estimate motor outputs and sensory inputs underlying spontaneous infantile movements, we used an inverse dynamics



**Fig. 1.** Research overview. (A) Motion capture of infantile spontaneous movements in the absence of external stimulation. (B) Fifty-one tracing markers on body parts and the estimated joint position relative to the parent and child link. (C) Estimated muscle activations and proprioceptive inputs using the infantile musculoskeletal model. (D) The directed binary matrix ( $288 \times 288$ ) indicating the presence of information flow among each sensorimotor signal at each time point. (E) Extraction of the sensorimotor modules using an infinite relational model. (F) Extraction of the sensorimotor state based on time-varying clustering. (G) An example of fluctuation in sensorimotor interactions. (H) A comparison of the spatiotemporal property of the sensorimotor interactions between neonates and infants.

approach, which is widely used to describe biomechanical systems (31, 32). To utilize this approach, we constructed a whole-body infantile musculoskeletal model based on an adult model and infantile skeletal specimen. These arrangements enabled the estimation of muscle activations and proprioceptive sensory inputs in 144 muscles throughout the body, resulting in 288 muscle-related information (Fig. 1C and *SI Appendix*, Table S1).

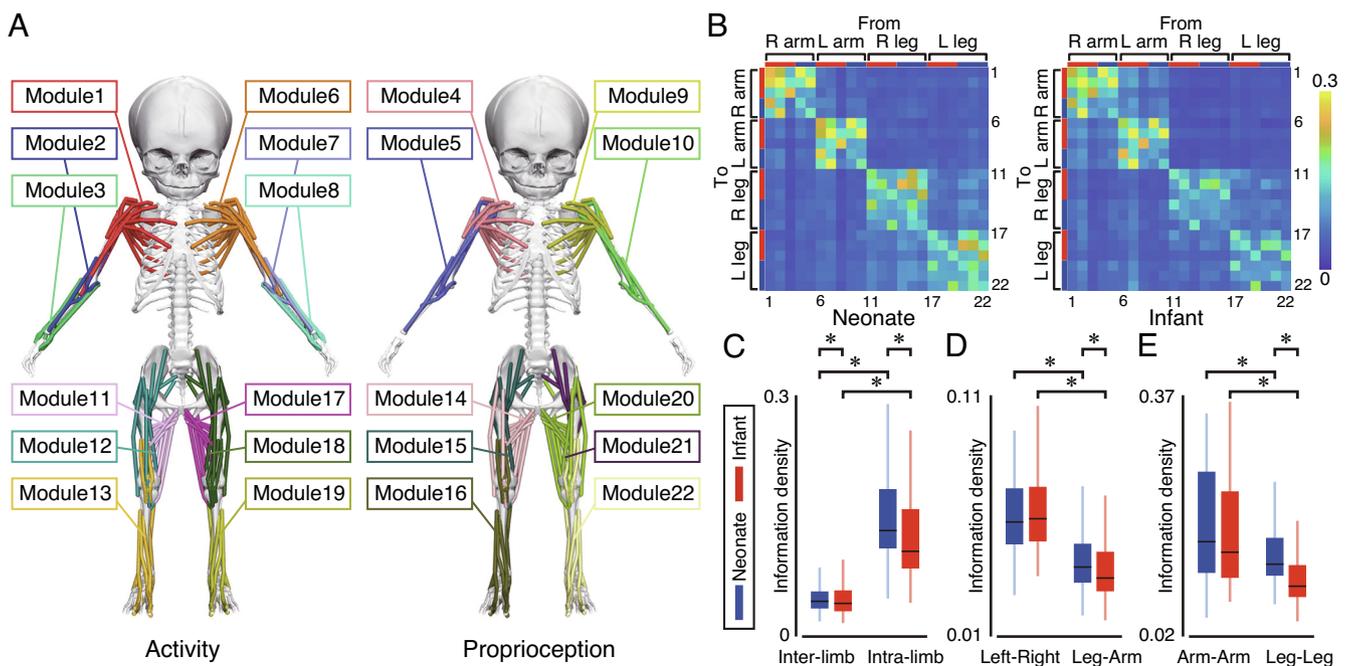
To delineate information structure regarding whole-body sensorimotor interactions, we calculated the information flows as sensorimotor interactions among the muscle activations and proprioceptive inputs via a sliding time-windowed Granger causality (33), which identifies directed functional interactions. Using a random permutation approach, we obtained a directed binary matrix (288 × 288), which indicated the presence of information flow within each sensorimotor pair at individual time points (Fig. 1D). Insignificant differences in the overall occurrence rate of information flow over the entire recording time were noted between the neonate and infant groups (95% bootstrap CI: 0.067 to 0.084 vs. 0.060 to 0.073). The distributions of sensorimotor information were macroscopically similar between the neonate and infant groups, with higher information flow within the limbs (*SI Appendix*, Figs. S3A and S4). Focusing on each sensorimotor pair, we found a convoluted distribution with some pairs increasing and other pairs decreasing significantly between the two groups, indicating difficulties in comprehension of developmental changes (*SI Appendix*, Fig. S3B), which suggests the necessity of extractive analysis to improve the interpretability of the muscle-pair-level results. Therefore, to understand the developmental changes in sensorimotor interactions, we aimed to extract spatial functional modules in the next analysis.

### Embodied Functional Modules in Sensorimotor Interactions.

To extract functional modules, we adapted the infinite relational

model (IRM) (34–36) for sensorimotor interactions among the muscle activations and proprioceptive inputs. The IRM, a nonparametric Bayesian model, extracts functional modules that interact with other modules coherently based on their information densities with direction. Finally, we extracted 22 sensorimotor modules consisting of body-dependent components (Fig. 2A and *SI Appendix*, Table S2). Each module comprised symmetrically placed muscles around the shoulder, elbow, wrist, hip, knee, and ankle joints. Except for two arm-related modules, nearly all modules comprised muscle activities or proprioceptive inputs (Modified Davies–Bouldin Index = 0.52, See *SI Appendix*, *Supplementary text*).

Based on the extracted sensorimotor modules, we obtained a 22 × 22 matrix at each time step (range: 0 to 1), which represented the information density of sensorimotor interactions among each module pair. To describe the general characteristics, we averaged the information density in the time domain as the emergence rate of sensorimotor interactions (Fig. 2B and *SI Appendix*, Fig. S5). The time-averaged information density in each module pair was substantially correlated between the neonate and infant groups ( $r = 0.774$  via Spearman's rank correlation, 95% bootstrap CI: 0.706 to 0.825). Moreover, the macroscopic structures were similar between these groups: a higher information density was observed in intra-limb (vs. inter-limb, Fig. 2C), left-right (vs. leg-arm, Fig. 2D), and arm-arm (vs. leg-leg, Fig. 2E). These results suggest that the limb combinations with high information densities in the neonatal period retain high sensorimotor interaction in later infancy. Those with low information densities in the neonatal period similarly retain a low sensorimotor interaction in later infancy. To verify whether and how developmental changes occurred in sensorimotor interactions, we then compared the neonate and infant groups focusing on each module pair.



**Fig. 2.** The sensorimotor modules and information density. (A) The IRM approach has extracted 22 sensorimotor modules. These modules are functionally coherent with each other in terms of their directed information density. Left modules only comprise muscle activities, whereas right modules only comprise proprioceptive inputs, except for modules 3 and 8, which also include proprioception inputs. (B) The time-averaged information density among each extracted sensorimotor module, based on an IRM in the neonate (Left) and infant (Right) groups. The columns and rows are ordered by module number, which are indicated below and right side of each matrix (*SI Appendix*, Table S2 shows module number.) Red lines denote the modules assigned to activity, and blue lines denote modules assigned to proprioception. L; left, R; right. (C) Differences in the inter- and intra-limb information density between the neonate and infant groups. (D) Differences in the inter-limb information density, focusing on pairs of body parts. (E) Differences in the intra-limb information density, focusing on pairs of body parts. Note; the asterisk (\*) in C, D, and E indicate significant differences with false discovery rate correction at  $q = 0.05$ .

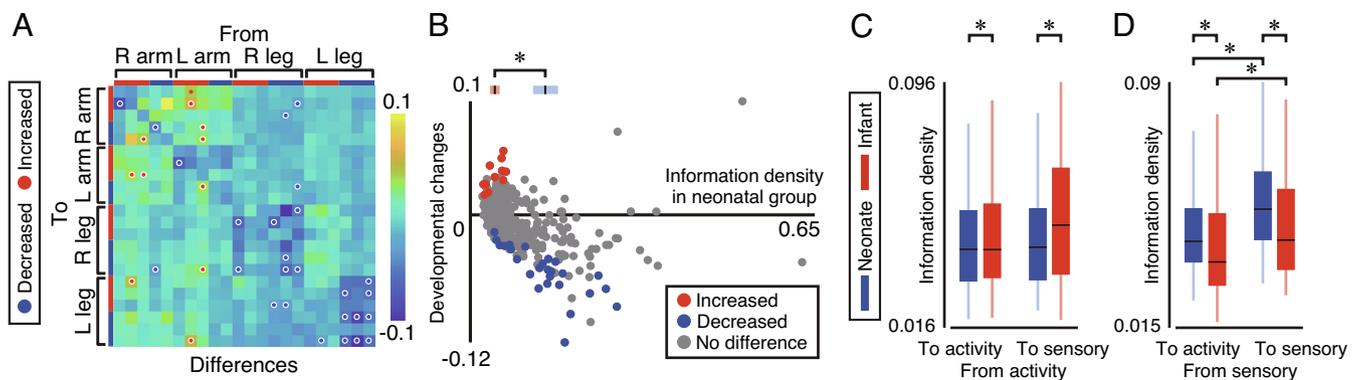
**Age-Related Changes in Sensorimotor Interactions.** In comparison between neonates and infants, we found differences in each module pair that were significantly increased and decreased (Fig. 3A, red and blue dots, respectively). An intriguing finding was that the whole developmental changes were inversely correlated with the information density of neonate group which presumably has a more naïve condition (Fig. 3B,  $r = -0.437$  via Spearman's rank correlation; 95% bootstrap CI:  $-0.515$  to  $-0.354$ ). Moreover, pairs with an increased information density had a lower density in the neonate group, whereas pairs with a decreased information density had higher density (Fig. 3B, 95% bootstrap CI:  $0.0367$  to  $0.0550$  vs.  $0.119$  to  $0.167$ ).

In terms of the combination of body parts, we found a decrease in information density for inter-limb, for intra-limb, for leg-arm, and for leg-leg between the neonate and infant groups (Fig. 2 C–E, 95% bootstrap CI of the mean difference:  $-0.0038$  to  $-0.0006$ ,  $-0.0292$  to  $-0.0180$ ,  $-0.0058$  to  $-0.0025$ ,  $-0.0400$  to  $-0.0286$ , respectively). Moreover, we found differences in modality-dependent sensorimotor interactions concerning inter-limb interaction. We identified an increase in the activity-driven information density both to activity and proprioception (Fig. 3C, 95% bootstrap CI of the mean difference:  $0.0009$  to  $0.0066$  and  $0.0032$  to  $0.0094$ , respectively), compared to a decrease in the proprioception-driven information density (Fig. 3D, 95% bootstrap CI of the mean difference:  $-0.0086$  to  $-0.0035$  and  $-0.0120$  to  $-0.0051$ , respectively). Similar trends can be seen in Fig. 3A, wherein sensorimotor module pairs with significant increases were primarily driven by muscle activity, whereas decreased pairs were driven proprioceptively (red and blue dots, respectively, in Fig. 3A). These findings indicated that sensorimotor interactions during infantile spontaneous whole-body movements exhibit developmental changes based on the combination or direction of body-dependent modules. On the other hand, comparisons of muscle activities and proprioceptive inputs at the module level between the neonate and infant groups revealed no significant differences.

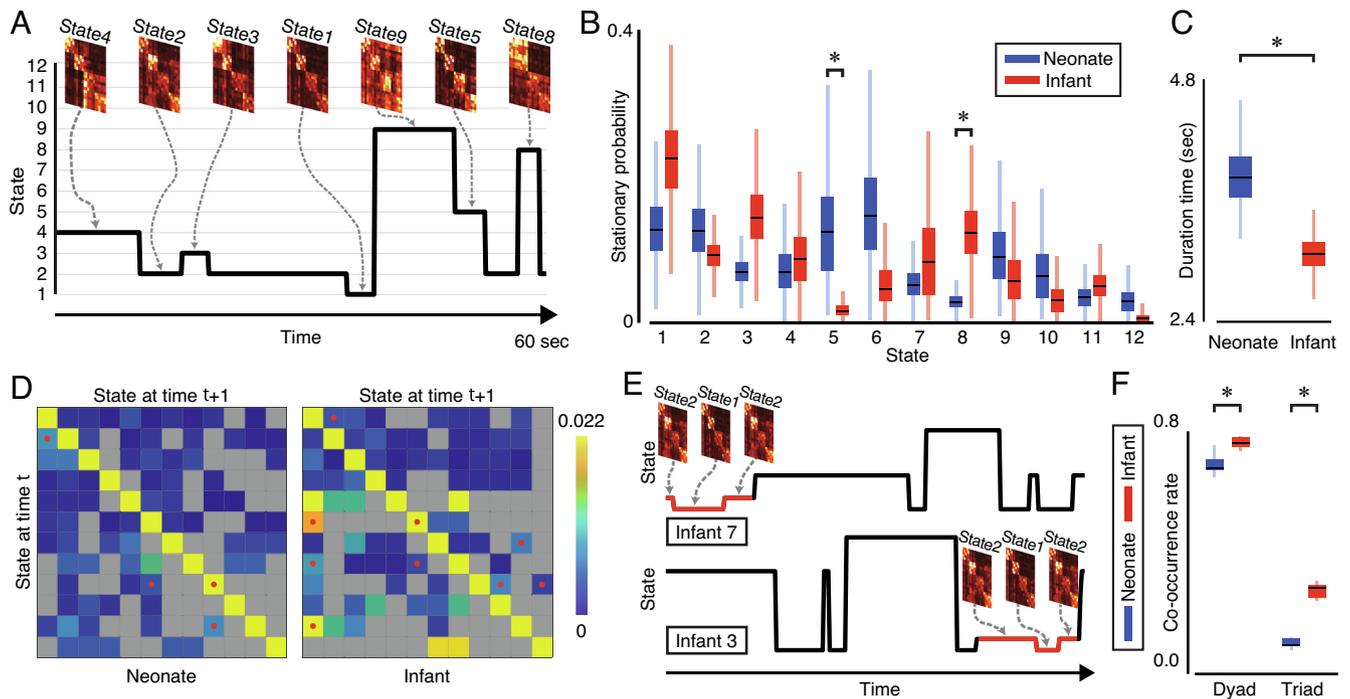
**Dynamic Sensorimotor Interactions.** The extracted modules represented an average fundamental sensorimotor interaction throughout the overall recording. However, infantile spontaneous movements have temporal fluctuations, thereby facilitating dynamic sensorimotor interactions. To assess the dynamic characteristics, we adapted spectral clustering based on an

ensemble non-negative matrix factorization as the time-varying clustering method, posterior to the IRM-based dimension reduction. This procedure identifies recurring patterns in sensorimotor interactions across participants in the time domain. Finally, we obtained 12 states and delineated a dynamic transition in sensorimotor interactions (SI Appendix, Figs. S13 and S14), expressing the spontaneous emergence of sensorimotor states, such as “sensorimotor wandering” in neonates and infants (Fig. 4A and SI Appendix, Fig. S15). The procedure revealed 136 and 152 state transitions in the neonate and infant groups, respectively, with a significant decrease in the time duration of each state (Fig. 4C, 95% bootstrap CI:  $3.35$  to  $4.35$  s vs.  $2.72$  to  $3.35$  s), suggesting that an infant was less likely to remain in one sensorimotor state and more likely to move to another. Thus, compared to a neonate, an infant was more prone to wander in the sensorimotor interactions. While the decrease in time duration, comparisons of the stationary probability of each state between the two groups showed similarity except states 5 and 8 (Fig. 4B). To identify whether each sensorimotor state had specific joint movements, we performed one-way analysis of variance, which revealed no significant differences in each joint angle velocity among the state. This result implied that externally observed joint movements do not always reflect sensorimotor interactions in neonates and infants.

To describe the developmental changes based on the properties of dynamic transition, we estimated group-level transition probabilities as a Markov chain (Fig. 4D). Together with the previous similarity in stationary probability, approximately 70% of the possible state transitions (with non-zero values) overlapped between the neonate and infant groups. The red dots in each transition probability matrix represent the points that exceeded the threshold generated by random permutation, indicating that when a participant is in one state, he or she then tends to transition to a certain state. They implied non-randomness and a constant tendency for state transitions in fluctuating sensorimotor interactions. To examine whether the transition probability matrix of neonate and infant group is far from random, we conducted the permutation test, in which the null hypothesis was that each matrix would have the same number of state transitions exceeding the threshold. These results clarified that the state transition of the infant group significantly differed from random ( $P = 0.0210$ ), whereas neonate group do not differ ( $P = 0.6776$ ).



**Fig. 3.** Comparison of information density between the neonate and infant groups. (A) Differences in information density among each sensorimotor module between the neonate and infant groups. The red and blue dots indicate significant increases and decreases, respectively, from the neonates to infants. L; left, R; right. We did not perform multiple-comparison corrections due to insufficient sample size for number of iteration analysis ( $22 \times 22 = 484$  iterations, see SI Appendix, Fig. S8). (B) Correlation between differences in information density from the neonates to infants and those of the neonates, displaying significant increases and decreases, as indicated in A. The blue lines and red lines indicate 95% confidential interval of the average, which shows significant differences ( $P < 0.05$ , Welch's  $t$  test). (C) Differences in the inter-limb information density, focusing on information direction from activity (i.e., from muscle activity). (D) Differences in the inter-limb information density, focusing on information direction from sensory (i.e., from proprioceptive input). Note; the asterisk (\*) in C and D indicate significant differences with false discovery rate correction at  $q = 0.05$ .



**Fig. 4.** The extracted state and fluctuations of the sensorimotor interactions. (A) An example of state transition in the sensorimotor interactions. (B) Stationary probability, calculated with bootstrap resamples. ( $*P < 0.05$ ; permutation test). (C) A comparison of the stay duration at each state between the neonate and infant groups. ( $*P < 0.05$ , Welch's *t* test) (D) The state transition matrix obtained using bootstrap resampling. The red dots indicate points that exceed the threshold generated by random permutation. (E) Sample of a state transition displaying a shared triad state sequence (red line: State2→State1→State2). (F) A comparison of the co-occurrence rate of repeated dyad triad state sequences per one sequence based on the jackknife mean ( $*P < 0.05$ , jackknife test).

**Shared Sequences in Sensorimotor State Transitions.** Furthermore, we aimed to assess the presence of a temporal pattern in spontaneous sensorimotor interactions and associated age-related changes. With regard to temporal patterns, we defined the dyadic and triadic state sequences based on previous and subsequent sensorimotor states when state transitions occurred (Fig. 4E). The repetition rate of each dyadic and triadic sequence pattern was calculated as the co-occurrence rate over the entire recording time and across participants. We consequently identified a higher co-occurrence rate of the dyadic and triadic state sequences in infants than in neonates (Fig. 4F; 95% jackknife CI: for dyadic, 0.557 to 0.684 vs. 0.698 to 0.746; for triadic 0.022 to 0.091 vs. 0.202 to 0.267). The co-occurrence of dyadic and triadic state sequences indicates shared sequences among other participants, indicating that infants had more common temporal patterns than did neonates.

## Discussion

Our primary findings included the embodied information structure and non-random fluctuations in sensorimotor interactions during infantile spontaneous movements. These features displayed age-related changes depending on the embodiment and direction of sensorimotor interactions. These findings indicated that early spontaneous movements elicit body-dependent sensorimotor modules, possibly leading to the acquisition of coordinated behavior, despite the involvement of muscles throughout the body. Furthermore, we observed increases in the shared sequences among participants in sensorimotor fluctuations, thus indicating that spontaneous movements contribute to temporal sensorimotor learning, without an explicit task or purpose. The results further indicated that early spontaneous movements have spatiotemporal characteristics analogous to spontaneous activity in the nervous system.

Researchers have investigated spontaneous whole-body movements in early developmental stages for their clinical utility, principally from a kinematic perspective. Recent advances in measurement technology have attracted further attention and research, with the potential to lead to the accurate prediction of developmental disorders, their automation, and a better understanding of neural maturation. In this study, we delineated spatiotemporal information structures regarding whole-body sensorimotor interactions in the early developmental stages. Our procedures demonstrated that early spontaneous movements elicited body-dependent modules in sensorimotor interactions (Fig. 2A). Animal and human studies have revealed that motor behavior involves a small set of primitive muscular control patterns called “motor primitive” (37, 38). A postulation is that an immature motor primitive already exists in early developmental stages and is established based on experience (19). In general, motor primitives are observed in cyclic or task-specific movements, such as walking or reaching, whereas our study supports that neonates and infants can acquire sensorimotor modules through open-ended movements involving the whole body simultaneously, even without an explicit purpose nor goal. This finding is similar to a previously proposed self-organization process (6). Moreover, the extracted modules comprised only muscle activities or proprioceptive inputs and implied independent sensorimotor components underlying infantile spontaneous movements. Nearly all research into infantile movements has focused on kinematic properties or muscle activities causing movement; however, our findings suggested that infantile spontaneous movements should be examined separately in motor outputs and sensory inputs.

Macroscopic structures of the time-averaged information density were similar between the neonate and infant groups (Fig. 2B), which was consistent with findings of previous studies that investigated longitudinal changes in the endpoints of limbs during

spontaneous movements (17, 39). This finding subsequently indicated that early spontaneous movements are generated by spontaneous neuronal activities with a common substrate, which activate general muscle activities that regulate sensory inputs via embodiment and the environment. However, age-related changes in whole information density were inversely correlated with the information density of neonates (Fig. 3*B*). Information density, which can be considered as the occurrence of sensorimotor interaction among each module pair, in the neonatal period probably represents the incipient sensorimotor interaction. If, as is commonly assumed, sensorimotor system development depends on the occurrence of sensorimotor interactions, then module pairs with high information density in the early stage should increase their density, thereby resulting in a positive correlation, contrary to our findings. However, the inverse correlation findings depicted in Fig. 3*B* implied that humans in early infancy developed movement by pursuing novel sensorimotor interactions, which is congruent with evidence for visual explorations with increasing attention to novel patterns during the early developmental stage (40).

Structural differences between neonates and infants revealed age-related changes in sensorimotor interactions depending on the combinations of body parts (Fig. 3*B* and *D*, intra-limb and leg-leg). Considering the modules reflected body functionality (Fig. 2*A*), the decrease in information density in our study indicated that infants tend to move their limbs according to sensorimotor interactions across rather than within body parts compared to that noted in neonates. Thus, humans in early infancy expand their fields of sensorimotor interactions from local to global networks. This finding was analogous to physiological studies that suggested developmental shifts from local to large-scale neuronal networks (9).

Moreover, we observed increased activity-driven information density and decreased proprioception-driven information density (Fig. 3*C* and *D*). Considering proprioception-driven information density as a muscle response to proprioceptive input, a decrease in the information density implied the disappearance of a primitive reflex. By contrast, sensorimotor interactions from muscle activity to proprioception occurred when an infant moved the limbs precedent to certain sensory inputs as if aiming toward the desired perception. Assuming these sensorimotor interactions traced the consecutive relationships among inputs and outputs in the sensorimotor system, incremental changes may reflect the emergence of an internal model (41), as suggested by studies evaluating involvement with early spontaneous movements (42). Age-related changes were inversely correlated with information density in neonates; therefore, sensorimotor interaction was spatially organized based on functionality or novelty rather than a straightforward experience.

Experimental studies evaluating vision development have revealed that the distributions of spontaneous neuronal activity patterns without external stimuli gradually become similar to those observed in the natural condition (43). Based on a Bayesian approach, this process is interpreted as the maturation of an internal probabilistic model, thereby suggesting statistical regularization through environmental interactions shapes the spontaneous activity reflecting prior expectations. Early sensorimotor interactions with inseparable spontaneous and evoked activities could similarly underlie a recursive process, thus resulting in the establishment of internal models. In this study, we speculated that infantile sensorimotor explorations resulted in the aforementioned findings regarding the inverse correlation between neonatal information density and developmental changes. Moreover, they may be a consequence of this process with an optimizing prediction error and conditional expectations (44, 45).

Together with the functional roles in the behavioral maturation process, early spontaneous neuronal activities reflected the existence of anatomical and functional neuronal connectivity. Furthermore, even neonates with unestablished cognitive function displayed fragmentary resting state networks observed in adults (46). Moreover, sensorimotor interactions facilitated learning about spatial constraints from the information generated by the musculoskeletal body, thereby shaping body-dependent modules; this phenomenon occurs similarly as increases in cortical structural-functional coupling in the resting state during early development (47). Thus, sensorimotor interaction is to the structure of embodiment what functional connectivity is to the brain's anatomical connectivity. This commonality emphasizes that infantile spontaneous movements induce embodied sensorimotor interaction, which guides local and global neuronal maturation before voluntary motor control.

In addition to stationary functional connectivity, recent studies have demonstrated time-varying fluctuations in spontaneous activities and their relationship with behavioral traits (48, 49). Non-random fluctuations in infantile spontaneous movements additionally link to functional connectivity in the resting state. It seems a contradiction that infantile spontaneous movements simultaneously exhibit both resting and moving characteristics; however, these data implied that infants wandered and pursued sensorimotor interactions, such as “mind-wandering” in the resting state, which is attributed to spontaneous cortical activities (50). We believe that fluctuation in early sensorimotor interaction provides an insight into the association between neural activity and early spontaneous movements.

Sensorimotor interaction fluctuations in neonates and infants exhibited similarities in the probability of both stationary and state transition. Structured and planned movements have already been identified in the human fetus (14, 51); hence, these similarities may imply that neonates and infants share common neural substrates that induce sequential spontaneous sensorimotor interactions. Furthermore, we observed a higher occurrence of dyadic and triadic state sequence patterns as well as higher non-randomness of the state transitions in infants than in neonates, indicating that infants had more structured sensorimotor interactions in the time domain. State sequence patterns co-occurred repeatedly across multiple participants; therefore, they may have emerged from a common neural substrate. By contrast, they may be learned under common constraints owing to an embodiment or environment, considering motor learning based on early sensorimotor experience observed in fetal rats and human infants (52, 53). Sensorimotor interactions are temporally organized in the early developmental stages through spontaneous whole-body movements. Our findings also support the hypothesis that infants seek and integrate the temporal structure of sensorimotor interactions, although their movements have no explicit objective.

We found the shared spatiotemporal patterns of sensorimotor interactions between the neonate and infant groups, indicating early spontaneous movements are generated by common substrate. The neural substrate that is relevant to triggering early spontaneous movements might be located in the spinal cord, brainstem, and motor cortex, thereby generating muscle activities (9). The maturation of the thalamocortical and corticothalamic systems, including transient subplate neurons, may have an important role in sensorimotor integration during spontaneous movements (5, 24). Previous studies, which reported spatiotemporal self-organization of myoclonic twitches in sleeping rat pups or human infants, also indicated thalamocortical function as relevant neural circuit (42, 54, 55). Differences exist between the sleep and waking

states, and between intra-limb and whole-body, although the mechanisms suggested in these previous studies would have some commonality with our results in terms of sensorimotor development. In addition, considering that twitch has a calibration role during sleep as these studies suggested, the awake movements we observed may reflect somewhat more conscious behaviors such as exploration.

In clinical fields, the presence of atypical movements is a prognostic biomarker of neurological disease or developmental disorders (24–26, 39). Our procedure, which focuses on information flow among muscle signals, would be potentially valuable in clinical research aiming to utilize as prognostic biomarkers as well as to understand behavioral origins. We observed spontaneous movements in the absence of external stimulation in the awake, active, and non-crying states. By contrast, unpleasant stimuli or emotionally unstable condition such as pain or anxiety can obviously change their movements. Such external stimuli could lead to a detrimental effect on subsequent sensorimotor development, especially if these situations are prolonged or repeated.

In this study, we estimated muscle activities and proprioceptive inputs among multiple whole-body muscles to quantify sensorimotor interaction. Musculoskeletal simulation provides muscle-related information that is difficult or impossible to measure (31, 32). It has been used for various tasks in animals and humans; however, only a few studies have been conducted on neonates and infants. Thus, the full establishment of estimation in future studies with measurement technological advancements is desirable. In addition, we measure the only 60 s of spontaneous movements from a total of 22 neonates and infants because of the complexity and difficulty of the experiment in which larger sample and longer data would have been desirable, if possible. Recent technology of motion capture is progressing rapidly, making it possible to solve these limitations in the near future.

Synthetic knowledge such as developmental psychology, neuroscience, and robotics, proposes that developmental changes in behavioral and neural dynamics modify the structural and functional networks in the brain, thus resulting in subsequent behavioral development (27–29, 56). Our findings suggested that the recursive developmental processes begin in early infancy with spontaneous movements. Moreover, our findings supported the hypothesis that early spontaneous activities denote some kind of origin of human variation, individuality, consciousness, and intentionality (27, 28, 57).

To conclude, we identified embodied information structures and non-random fluctuations in sensorimotor interactions during early spontaneous movements. Thus, early open-ended movements contribute to sensorimotor development in a self-organizing manner, which has common aspects with the maturing neuronal system. Our procedure encourages further investigations to deepen our understanding of the mechanisms underlying early sensorimotor development.

## Materials and Methods

**Participants.** We enrolled 12 healthy neonates aged  $\leq 10$  d and ten 3-mo-old infants. None of them or their first-degree relatives had neurological impairments. This study was approved by the Office of Research Ethics at The University of Tokyo and Kyoto University and was conducted in accordance with the tenets of the Declaration of Helsinki and its amendments. Written informed parental consent was obtained before the procedures.

**Motion Capture.** We conducted a full-body motion capture of infantile spontaneous movements in the absence of external stimulation for 60 s in the awake, active, and non-crying states. Moreover, we recorded the three-dimensional positions of 51 markers using 12 infrared cameras (Flex 3, FPS: 100; OptiTrack) at 100

fps. Thereafter, we placed a set of three markers to define the relative position of each body link connected through the joint. The target joint comprised the shoulder, elbow, hand, hip, knee, and ankle. The captured body link included the head, trunk, upper arm, forearm, hand, pelvis, thigh, calf, and foot. The joint position was relative to both the parent and child link and was estimated by the least-squares method minimizing the positional error over the entirety of the recording time (SI Appendix, Fig. S2). We obtained information on relevant properties concerning the body shape of each infant, namely the length, joint position, joint anchor, and joint axis. We subsequently estimated 12 joint movements with 26 degrees of freedom via inverse kinematics using OpenSim (31). These joint movements were low-pass filtered at  $< 3$  Hz for the subsequent analysis.

**Estimation of Muscle Activities and Proprioceptive Inputs.** The estimated kinematic data were input into the OpenSim. We estimated the muscle length and muscle activities within the musculoskeletal model, which was segmented into each limb (upper, lower, left, and right) and modified based on the shape of the body part and the body weight of each infant. We computed the proprioceptive input,  $I$ , based on a spindle model and muscle stretch,  $S$ , using the following equation ((58)):

$$I = 2 * S + 4.3 * \text{sign}(\Delta S) \times |\Delta S|^{0.6}.$$

**Estimation of Information Flow.** We estimated sensorimotor interactions by calculating the information flow between all muscle pairs about the muscle activities and proprioceptive sensory inputs using Granger causality with first differences. To quantitatively assess whether the occurrence of the binarized information flow computed at each time point was similar, we calculated pairwise Granger causality by using the MVGC toolbox (33). To compute the dynamic information flow, we applied a sliding window approach together with the Tukey window. Each signal following a 5-Hz low-pass filter and down-sampling at 10 Hz was segmented into epochs of 10 s, with sliding-in steps of 0.1 s. The window size was determined, based on the main power frequency of the muscle activities and proprioceptive inputs (0.1 to 0.5 Hz). Following quantification of information flow, which has non-stationary and various temporal characteristics, we binarized the derived data via permutation testing to make them comparable among each time step or signal pair. An iterated amplitude-adjusted Fourier transform surrogate methodology, which generates random surrogate data with preserving the original frequency power (59), was applied to permutation testing. The null hypothesis in this test was that the obtained data come from the random distribution generated by random surrogating of the original data. If the obtained data has a higher value than 99 percentiles of random distribution, the null hypothesis was rejected. Thus, we obtained a  $288 \times 288$  binarized directed information flow matrix at each time step. We examined the effects of window size and thresholding value as a verification of robustness (SI Appendix, Figs. S11 and S12).

**Extraction of Sensorimotor Modules.** To extract the sensorimotor modules, we adapted the IRM, which extracts functional coherent modules based on their densities about the information flow (34–36). We performed subsampling, including the selection of the local maxima of similarity based on mutual information among each binary matrix to reduce redundancy. After extracting 22 modules, we calculated the density of sensorimotor interactions for each module. We obtained a  $22 \times 22$  matrix at each time step (range: 0 to 1), which demonstrated the information density of the sensorimotor interactions. The time-average of this information density indicated the emergence rate of sensorimotor interactions among the sensorimotor modules.

**Extraction of Temporal State.** We adopted ensemble spectral clustering based on orthogonal non-negative matrix factorization (ortho-NMF), as the time-varying clustering methodology to analyze time-varying aspects of the information density of sensorimotor interactions. Basic NMF decomposes a non-negative matrix  $X$  ( $p \times n$  matrix) into two low-rank non-negative matrices, namely  $F$  ( $p \times k$ ) and  $G$  ( $k \times n$ ), with the residual error of  $E$  ( $p \times n$ ) (60). Ortho-NMF with the additional factor  $S$  ( $k \times k$ ) absorbs the different scales of  $X$ ,  $F$ , and  $G$  and leads to the following rigorous clustering interpretation:  $X = FSG + E$  (61).  $G$  indicates the weight of  $F$ ; thus, the largest coefficient in the  $i$ -th column of  $G$  indicates the cluster pertaining to the aforementioned data point (62). We determined the rank number based on the information criteria (IC) defined by Bai et al., which

gives precise estimates of the number of factors when both of feature and time dimensions are large, as follows (63):

$$IC(k) = \ln(\|E(k)\|) + k \frac{p+n}{pn} \ln \frac{pn}{p+n},$$

in which  $E(k)$  is the sum of the squared residual at  $k$ . Subsampling was conducted and included the selection of the local minima of Euclidean distance among each information density of sensorimotor interactions to reduce redundancy. To obtain the clusters at each time step, ortho-NMF with  $k = 12$  was iterated 10,000 times for calculating the information density of sensorimotor interactions considering Gaussian noise. Eventually, we conducted spectral clustering considering coincidence probability calculations and obtained 10,000 clustering results at each time step.

**Data, Materials, and Software Availability.** The source data of all figures are available at UTokyo Repository (<https://doi.org/10.15083/0002005864>) (64).

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