Neural Mechanisms of Mental Processing: From Evoked Brain Activity to Generative Brain Activity

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Abstract

The traditional computer metaphor has employed evoked brain activity as the primary means to investigate the neural mechanisms underlying mental processing. Extensive research has revealed that evoked brain activity does not constitute the principal component of brain activity; rather, it interacts with and adaptively evolves alongside the more dominant spontaneous brain activity. Consequently, neither evoked brain activity alone nor the static interaction between evoked and spontaneous brain activity can effectively elucidate the neural mechanisms of mental processing. To address this predicament, the enactive cognition theory posits that brain activity exhibits unity and agency, regulating its own patterns of activity by minimizing the discrepancy between expectation and stimulus to adapt to continually changing contexts. The transformation of research paradigms is ushering cognitive neuroscience into a new era characterized by greater scientific rigor and humanistic orientation.

Full Text

Brain Mechanisms of Psychological Processing: From Evoked Brain Activity to Enactive Brain Activity

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Abstract

The traditional computer metaphor has long treated evoked brain activity as the primary means for exploring the neural mechanisms underlying psychological processes. However, accumulating evidence reveals that evoked activity represents only a minor fraction of total brain activity, interacting with and adaptively evolving alongside the far more dominant spontaneous brain activity. Consequently, neither evoked activity alone nor static characterizations of their interaction can effectively reveal the brain mechanisms of psychological processing. In response to this dilemma, enactive cognition theory proposes that brain activity is unified and agentic, continuously adjusting its own patterns to minimize the discrepancy between predictions and stimuli, thereby adapting to ever-changing contexts. This paradigm shift is propelling cognitive neuroscience toward a more scientific and humanistic new era.

Keywords: brain mechanisms; cognitive neuroscience; evoked brain activity; spontaneous brain activity; enactive brain activity; psychology

1. Introduction: The Crisis of Evoked Brain Activity

Task-evoked brain activity constitutes a fundamental experimental paradigm for investigating the neural mechanisms of psychological processing. According to the computer metaphor, identical inputs should produce identical outputs; yet the brain responds differently to the same input depending on its internal state at the moment of stimulation—that is, fluctuations in spontaneous brain activity [?, ?]. Major brain imaging techniques such as functional magnetic resonance imaging (fMRI) activation and event-related potentials (ERPs) assume negligible interaction between evoked and spontaneous brain activity, employing the general linear model (GLM) to characterize evoked responses and thereby elucidate the neural basis of cognition [?, ?]. This model posits that stimulus-evoked and spontaneous activities process information in parallel, with effects that are linearly additive; inter-trial variability in evoked responses can be explained by random fluctuations in spontaneous activity, which can be canceled out through trial averaging [?, ?]. The parallel processing assumption holds that psychological experiments can isolate stable task effects by eliminating interference from spontaneous fluctuations, while also treating spontaneous and evoked activities as independent. This view implies that spontaneous brain activity develops independently of learning and experience, violating the fundamental principle of neuroplasticity. Neuroplasticity necessitates interaction between spontaneous and evoked brain activity, making task effects dependent on their adaptive co-evolution and rendering it impossible to eliminate spontaneous influences through simple averaging.

In reality, changes in brain activity around stimulus presentation primarily reflect alterations in spontaneous activity. Spontaneous brain activity consumes 20% of the body’ s energy intake, far exceeding the 2-4% cost of cognitive effort [?, ?]. Simulation studies by Chen and Gong (2019) demonstrate that 80% of stimulus-evoked responses arise from changes in dynamic spontaneous activity, with only 20% attributable to external stimulation. Lynch et al. (2018) compared functional connectivity (FC) during movie watching and rest, finding that differences were driven primarily by reduced FC in spontaneous activity, with task-evoked FC explaining less than 2% of the variance. Shimaoka et al. (2019) applied grating stimuli to mice and found that spontaneous activity in bilateral visual cortex could explain 60% of inter-trial variability. Additionally, the low signal-to-noise ratio of ERP and activation signals indicates that spontaneous activity far exceeds evoked activity, and investigating the functional information embedded within spontaneous activity has become a cutting-edge research frontier [?, ?, ?, ?].

These findings collectively demonstrate that studying evoked brain activity in isolation cannot effectively reveal the neural mechanisms of psychological processing. An increasing number of researchers have shifted their focus from evoked activity to spontaneous activity and its dynamic relationship with evoked responses [?, ?, ?, ?, ?, ?]. Enactive cognition, as the third generation of cognitive science, further proposes that only one functional activity exists before and after stimulus presentation: the brain’ s trajectory through a multidimensional functional space [?, ?, ?]. These developments pose a serious challenge to traditional views of evoked activity, calling for revolutionary changes in experimental paradigms and analytical techniques to propel cognitive neuroscience into a new era.

2. Similarities and Differences Between Spontaneous and Evoked Brain Activity

Spontaneous brain activity emerges with the development and maturation of newborn neurons, establishing coordinated activity patterns among neuronal ensembles that are crucial for forming appropriate neural connections during development [?, ?]. Early brain development is largely constrained by genetic and physical principles while being continuously reshaped by sensory stimulation [?, ?]. According to Hebb’ s rule of “fire together, wire together,” repeated exposure to natural images leads to recurring activation patterns in spontaneous activity, forming specific local connections to represent naturally occurring stimuli and leaving traces in brain networks [?, ?].

At the level of single-neuron functional connectivity, the average influence of neuronal ensemble activity on single-neuron firing is remarkably similar under both resting and stimulation conditions. At the ensemble representation level, spontaneous and evoked activity patterns also show high similarity [?, ?]. Intracranial EEG recordings reveal that spontaneous activity in the dorsal anterior insula shares remarkably similar spectral characteristics with activity evoked during sustained attention tasks, with pupil dilation occurring at comparable latencies, indicating shared physiological mechanisms [?, ?]. At the macroscopic level, independent component analysis of large-scale brain activation databases shows that resting-state networks (RSNs) overlap substantially with task-evoked networks in spatial topography [?, ?], and these structures also closely resemble task co-activation networks [?, ?].

Researchers have proposed three possible explanations for the consistency between spontaneous and evoked activity: first, that spontaneous patterns reflect co-activation patterns formed through long-term experience; second, that spontaneous activity originates from spontaneous cognitive processes during conscious wakefulness; and third, that both are constrained by brain structure [?, ?]. However, no study has yet determined which view best explains their similarity.

Conversely, other research indicates that spontaneous and evoked activity patterns differ substantially. Temporally, large-scale neuronal ensemble activity concentrates in the infra-slow (<0.1 Hz) frequency band, peaking around 0.01 Hz [?, ?, ?], forming a stable temporal framework for brain function [?, ?]. During tasks, however, infra-slow oscillations are strongly suppressed while brain signals shift to higher frequencies to accommodate rapid psychological processing [?, ?, ?]. Spatially, spontaneous activity exhibits distinctive network structures that persist across different task-evoked activities, while evoked activity additionally shows both task-general and task-specific network configurations [?, ?, ?]. Moreover, cognitive tasks alter activity intensity and functional connectivity in task-irrelevant regions and even globally [?, ?, ?], resulting in higher global and local efficiency in evoked compared to spontaneous activity [?, ?, ?, ?, ?]. In terms of information transmission, thalamocortical circuits display different activity patterns during spontaneous versus evoked states. For instance, in rats presented with auditory stimuli, thalamocortical communication is enhanced, whereas it nearly disappears in the absence of stimulation, with intracortical communication increasing instead [?, ?]. Furthermore, after visual, auditory, or tactile stimulation in mice, information transmission trajectories become simpler and more stereotyped, with evoked activity amplitude and transmission speed increasing with stimulus intensity [?, ?]. These findings demonstrate distinct spatiotemporal characteristics between spontaneous and evoked brain activity.

Thus, spontaneous and evoked brain activity share commonalities while maintaining distinct features. Bolt et al. (2017) note that only a few task types have been used to examine their differences, suggesting that actual disparities may be far greater than currently detected. Laumann and Snyder (2021), after reviewing multiple literatures, found that spontaneous activity reflected in BOLD signals relates more closely to neuroplasticity and homeostasis than to dynamic changes in cognitive content. They identified three manifestations of the dissociation between spontaneous activity and cognition: first, BOLD signal topography remains intact during slow-wave sleep and even anesthesia, states with minimal or absent cognitive activity; second, cognitive tasks produce minimal changes in spontaneous activity connectivity patterns; and third, spontaneous cognitive activity varies substantially across scanning sessions while functional connectivity remains relatively stable [?, ?].

These findings indicate that spontaneous activity patterns remain relatively stable in the short term, constrained by physical pathways formed by neural fibers, and undergo plastic changes only over longer timescales, with cognitive perturbations representing a minor component. Consequently, the interaction between spontaneous and evoked activity can be understood as a trade-off between functional stability and plasticity, with their interaction patterns revealing rules and directions of brain functional evolution. This also suggests that spontaneous and evoked brain activities may not map one-to-one onto spontaneous and evoked cognitive activities. Arousal levels fluctuate during cognitive tasks, and mind-wandering involves spontaneous yet goal-directed processing encompassing numerous changing mental contents [?, ?]. These mental activities interact complexly with task-evoked processes [?, ?], implying that cognitive mechanisms cannot be captured through simple linear summation methods.

3.1 Influence of Spontaneous Brain Activity on Evoked Brain Activity

Spontaneous brain activity constrains evoked activity through multiple mechanisms. Early research focused on how EEG phase in , , , and bands influences visual processing efficiency, given that neuronal ensemble excitability and inhibition correspond to different phases of oscillatory activity [?, ?]. Recent studies have revealed that prestimulus spontaneous EEG activity predicts distinct aspects of cognition through phase, amplitude, and scale-free characteristics. For example, the phase of 5-40 Hz traveling waves generated by spontaneous activity in marmoset extrastriate cortex predicts both the intensity of task-evoked responses and perceptual sensitivity to ambiguous stimuli [?, ?]. Two studies using magnetoencephalography (MEG) and electroencephalography (EEG) found that prestimulus power significantly predicts consciousness level for weak stimuli but not perceptual sensitivity [?, ?, ?]. The power-law exponent (PLE) of scale-free characteristics in spontaneous anterior cingulate activity correlates positively with touch-evoked response strength [?, ?]. Both scalp EEG oscillation power and scale-free activity predict cognitive processing speed, yet only the latter remains predictive when the two are separated [?, ?]. These findings suggest that different aspects of cognitive processing—speed, accuracy, sensitivity—rely on distinct neural mechanisms with unique sensitivity indices. Just as measuring different physical quantities requires different tools, measuring different psychological constructs requires appropriate indicators. While children' s height and weight correlate highly, measuring height does not substitute for measuring weight; yet psychology frequently uses single indicators (e.g., ERP) to assess diverse processing mechanisms. Developing diverse, high-validity indicators for psychological processes represents a fundamental challenge for the field.

Beyond oscillatory properties, spontaneous activity influences evoked activity differently across temporal scales and durations. Spontaneous and evoked activities show negative interactions at high frequencies (-low), where higher prestimulus power produces stronger post-stimulus desynchronization, lower amplitudes at 300-400 ms, and reduced inter-trial variability. Conversely, positive interactions occur at low frequencies (-), where higher prestimulus power enhances event-related synchronization (ERS), increases amplitudes at 150-250 ms, and elevates inter-trial variability. These opposing interactions primarily involve neural oscillations rather than scale-free activity [?, ?]. Another study found that greater prestimulus and (8-30 Hz) power enhances neural inhibition, reducing early (<200 ms) ERP components through functional suppression, while stronger prestimulus oscillations produce greater post-stimulus power suppression, increasing late (>400 ms) ERP components through baseline-shift mechanisms [?, ?]. A study combining neuronal calcium imaging, optical imaging, and hemodynamic imaging revealed that ~0.1 Hz spontaneous neuronal activity negatively correlates with sensory-evoked calcium activity, with spontaneous and evoked hemodynamic activities showing inverse interactions while evoked hemodynamic and calcium activities correlate positively [?, ?].

Extensive research demonstrates that different cognitive and neural processes operate on distinct timescales, forming complex network structures through cross-frequency coupling [?, ?]. This underscores the need to investigate cognition and brain function across appropriate spatiotemporal scales; while epiphenomena may be discovered at inappropriate scales, critical cognitive mechanisms remain elusive. In summary, spontaneous activity influences evoked activity spatiotemporal patterns in systematic ways, and exploring the spatiotemporal characteristics of cognition-neural correspondences represents a core mission for elucidating psychological processing mechanisms.

3.2 Influence of Evoked Brain Activity on Spontaneous Brain Activity

Although evoked brain activity is relatively weak, it effectively perturbs spontaneous activity. Current research indicates that evoked activity primarily impacts spontaneous activity through functional connectivity (FC) and global activity patterns. The effects on FC show consistency across tasks: flexible networks such as frontoparietal, default mode, and attention networks typically exhibit task-dependent FC enhancement [?, ?, ?]. Conversely, intra-network FC generally decreases, with active, conscious task engagement producing stronger desynchronization [?, ?]. Overall, spontaneous FC predominantly decreases during cognitive tasks [?, ?]. This reduction does not indicate diminished interregional communication but rather reflects decreased shared spontaneous activity; suppressing spontaneous activity reduces neural noise and enhances task signal precision [?, ?]. Numerous studies have shown that cognitive tasks reduce neural variability [?, ?, ?, ?, ?] and reorganize FC [?, ?, ?, ?]. Thus, beyond enhancing target stimuli and suppressing distractors during attention, the brain employs a comprehensive reinforcement-inhibition mechanism that suppresses spontaneous FC to augment task-relevant FC and optimize behavior.

In addition to FC suppression, evoked activity alters global spontaneous activity patterns. Deneux and Grinvald (2017) investigated how brief sensory input modifies internal brain dynamics, finding that even single whisker stimulation in anesthetized rats markedly disrupts excitatory and inhibitory states in somatosensory barrel cortex, with stimulated functional columns failing to enter excitatory states for several seconds. After several minutes of sequence learning, neural activity patterns during stimulation replay during subsequent spontaneous activity, with reverberations lasting minutes [**?**, **?**]. Lewis et al. (2009) trained participants on attention to the left lower visual field, discovering that after 2-9 days, resting-state FC increased between the right superior occipital gyrus and attention-related regions while other visual cortex FC remained unchanged. Berkes et al. (2011) found that during ferret development, spontaneous activity patterns became more similar to natural-stimulus-evoked patterns but less similar to artificial stimuli (e.g., gratings). Avitan et al. (2021) observed that in zebrafish, developmental trajectories of spontaneous and spot-evoked activity were similar, but their spatial similarity decreased with development; evoked activity showed higher co-activation levels and information dimensionality across all developmental stages. These findings suggest that evoked activity generates new information dimensions and induces spontaneous activity to explore and assimilate this high-dimensional information, reshaping spontaneous patterns across timescales from immediate activity to developmental growth. From this perspective, the ubiquitous negative interaction between evoked and spontaneous activity can be understood as evoked activity suppressing original spontaneous dimensions and redirecting them toward new dimensions, continuously remodeling spontaneous activity patterns. This mechanism reflects the brain’ s characteristics as a complex system and may provide novel insights into the neural mechanisms of learning and memory.

3.3 Interaction Between Evoked and Spontaneous Brain Activity

The influence of spontaneous activity on evoked activity means that measured evoked responses vary with the brain’ s spontaneous state. Conversely, evoked activity’ s influence on spontaneous activity means that spontaneous patterns vary with task context, which in turn affects evoked activity, creating a cyclical interaction. During this cycle, dynamic spontaneous activity actively adapts to enhance external stimulus processing efficiency, while external stimuli modulate and reset spontaneous activity trajectories [**?**, **?**]. Chen et al. (2020) found that single-stimulus-evoked Ca^{2} transients were stronger at the trough (inhibitory phase) of spontaneous Ca^{2} oscillations, while stimulation reset spontaneous neural oscillation phase to the peak (excitatory phase), indicating that negative interactions are co-realized by both processes. Stringer et al. (2019) proposed that “noise” during stimulus presentation is behaviorally driven and detectable brainwide. They extracted over 100 latent behavioral states from spontaneous activity in mouse visual cortex, which fluctuated with ~200 ms periodicity; externally evoked activity did not interrupt these spontaneous states but instead 叠加 ed orthogonally. At the neuronal population level, dimensions encoding motor variables overlapped with those encoding visual stimuli in only one dimension, integrating over a 1-second timescale. Furthermore, the interaction between evoked and spontaneous activity is modulated by serotonin (5-hydroxytryptamine, 5-HT). Serotonin, primarily secreted by dorsal and median raphe nuclei and widely projecting to cortical and subcortical regions, enables fine-tuned modulation of spontaneous and evoked activity and their cross-network integration through differential distribution of inhibitory and depolarizing 5-HT receptors across cortical cell types [?, ?]. Azimi et al. (2020) found that 5-HT1A receptors suppress spontaneous activity in visual cortex while 5-HT2A receptors suppress visual-evoked responses, allowing serotonergic input to differentially inhibit spontaneous and evoked activity and thereby regulate their relationship.

Although bidirectional influence between evoked and spontaneous activity is theoretically necessary, empirical research remains limited. A few studies suggest that bidirectional influences occur simultaneously. If so, studies examining unidirectional effects face fundamental logical problems: while one process influences another, it simultaneously receives reciprocal influence, precluding the existence of two fixed states for studying their interaction. In other words, the brain mechanisms of psychological processing cannot be effectively elucidated through evoked activity alone or through unidirectional influences, but must instead be viewed as a continuously evolving whole—a perspective that aligns perfectly with enactive cognition theory.

4. Beyond Spontaneous and Evoked: Enactive Brain Activity

Enactive cognition represents a new orientation in cognitive science following information processing and embodied cognition [?, ?, ?]. Within the enactive framework, predictive-processing theories posit that individuals interact with the world primarily through predictions or expectations, with the brain constantly adjusting and readjusting to construct and maintain task-relevant coordinated activity for environmental equilibrium [?, ?, ?, ?]. Thus, evoked brain activity is not a novel, independent process but rather a perturbation of spontaneous activity itself. In other words, brain activity is not evoked but spontaneous and enactive. Pezzulo et al. (2021) further argue that spontaneous brain activity constitutes the dynamic foundation for top-down generative models (probabilistic models describing data generation, termed predictions and attention in task and rest contexts) that predict cognition and behavior. Specifically, when performing tasks, the brain prepares top-down for processing particular stimuli and actions; during rest, brain activity is not limited to reactivating previous task patterns but prepares the brain to process a broader range of stimuli and actions for future environmental interactions. The brain' s generative model may simulate the "body in the world" along two dimensions—externally oriented behavior and internally oriented interoception—forming specific functional organizational patterns [?, ?], which aligns with Laumann and Snyder' s (2021) finding that spontaneous activity encompasses neuroplasticity, homeostasis, and real-time cognitive activity.

Mathematical models provide specific formulations of enactive brain activity and successfully explain state changes in response to external stimuli. Dynamical systems theory conceptualizes the brain-body-environment as a composite system of coordinated components [?, ?]. Such systems exhibit criticality—a state of interaction between complete asynchrony (disorder) and complete synchrony (order). The brain displays critical system characteristics at rest [?, ?] but subcritical dynamics during attention-demanding tasks [?, ?]. Subcritical dynamics correspond to stronger global synchronization and reduced dynamic range, decreasing responsiveness to diverse inputs and minimizing task-irrelevant interference. In other words, spontaneous activity can access multiple possible states, while external input drives the system into a specific state, reducing variability [?, ?]. Reduced variability can be understood as brain regions establishing a mutually constraining system that enters and maintains a task-appropriate functional configuration [?, ?, ?, ?]. This transition from multiple possible states to a specific task state primarily manifests as membrane potential oscillations between excitatory and inhibitory states [?, ?], which constitute slow cortical potentials correlated with BOLD signals [?, ?]. Therefore, fMRI activity may reflect low-frequency transitions between brain states [?, ?, ?, ?].

Similarly, Bayesian theory suggests that spontaneous activity maintains internal representations of all possible external environments by sampling numerous states, forming predictions or Bayesian priors. Once combined with sensory information representing the true state of the external world, priors become posteriors, embedding less uncertainty and thereby constraining the number of sampled states [?, ?]. This view posits that spontaneous activity plays an active role in sensory processing, with brain networks continuously attempting to infer environmental states, exploring all possibilities from accumulated experience even during rest or sleep [?, ?].

Friston (2010) proposed the free-energy principle (FEP) as a unified explanatory framework for brain activity as a complex system. FEP suggests that the brain, like any organism, is a self-organizing system that engages in adaptive activities to maintain survival and reproduction. Rather than being a passive sensory input device, it operates as a predictor conforming to generative models, minimizing prediction error through recursive processes that match internally generated priors with externally generated stimuli.

In recent years, numerous empirical studies have emerged supporting these models, demonstrating that brain activity patterns are control-oriented rather than merely representing the external world. Spontaneous activity thus represents a collection of brain states formed through the continuous internalization of perception-action loops, which can be automatically activated when needed in the future [?, ?]. The generative model endows the brain with agency, theoretically ensuring the unity between stability (determined by structure and experience) and plasticity (determined by environmental adaptation) in brain activity.

5. Conclusion: Toward Transformation

Because spontaneous brain activity constitutes the majority of brain activity and interacts reciprocally with evoked activity, neither relatively weak evoked responses nor static characterizations of their interaction suffice to reveal the neural mechanisms of psychological processing. Enactive cognition offers a solution: integrating spontaneous and evoked brain activity into unified enactive brain activity, an approach supported by empirical research and mathematical models that is guiding the study of psychological processing mechanisms toward revolutionary change.

First is the transformation of research paradigms. Finn (2021) notes that human brain imaging has entered its third wave: from traditional task paradigms to resting-state designs and now to integrated task-rest designs, with dynamic changes in brain activity across states being the core focus. In other words, integrated designs prioritize explaining how brain activity dynamically changes with context within a unified framework, rather than opposing spontaneous and evoked activity. Additionally, steady-state experimental designs that present tasks at fixed intervals (e.g., every 10 seconds) are being used to probe spatiotemporal characteristics of specific psychological processes [?, ?, ?, ?]. Steady-state designs provide an invariant context that allows the brain to focus on specific psychological processing while minimizing inter-trial expectation changes and reducing variability across and within trials.

Paralleling these paradigm shifts, new analytical methods have emerged. For instance, Simony et al. (2016) proposed inter-subject functional connectivity (ISFC) based on continuous naturalistic stimuli (e.g., movies, music) to extract task-evoked FC while excluding spontaneous activity or non-neuronal noise. The logic is that for any given brain region pair, correlations between one subject' s time series in one region and another subject' s time series in another region reflect only task-related activity rather than individual differences or within-subject noise [?, ?]. These paradigm and methodological transformations will inevitably change our understanding of psychological processing mechanisms and propel cognitive neuroscience into a new era.

Second is the transformation of scientific rigor in research metrics. Traditional evoked-activity research suffers from low signal-to-noise ratios and large inter-trial variability, yielding poor result reliability [?, ?]. A meta-analysis by Elliott et al. (2020) reported that the average test-retest reliability of task-state activation was only 0.397, with region-of-interest activation reliability ranging from 0.067-0.485. Due to publication bias and over-reliance on null hypothesis significance testing, psychological research also faces a severe reproducibility crisis [?, ?]. The Open Science Collaboration replicated 100 studies published in 2008 across three major psychology journals, finding that 64% failed to produce significant results, with significantly reduced effect sizes in those that did [?, ?].

Draheim et al. (2019) argue that variability in participant strategies and unstable measurement metrics (e.g., speed-accuracy trade-offs) are primary factors limiting the reliability of psychological experiments. Enactive cognition abandons dependence on weak evoked signals and unstable inter-trial variability, instead investigating psychological processing mechanisms from the holistic, dynamic perspective of enactive brain activity to comprehensively capture dynamic changes in both psychological processes and neural signals, thereby effectively addressing the reproducibility crisis and enhancing scientific rigor.

Third is the transformation of research ethics. Due to the widespread negative interaction between spontaneous and evoked activity, the "stimulation-evoked" research orientation substantially suppresses spontaneous brain activity. For example, rhythmic stimulation induces steady-state responses but reduces spontaneous activity at corresponding frequencies [**?**, **?**], and drug addiction leads to reduced or eliminated endogenous dopamine expression [**?**, **?**]. Thus, stimulation-oriented brain intervention techniques likely produce side effects by suppressing spontaneous activity. By emphasizing agency, enactive cognition ensures the brain's subjectivity, thereby transforming the status of "participants" in psychological research and promoting ethical advancement.

In summary, research on the brain mechanisms of psychological processing faces a severe crisis, yet this deepening investigation has spawned the new orientation of enactive cognition, providing crucial opportunities. The flourishing development of enactive cognition will undoubtedly propel cognitive neuroscience toward a more scientific and humanistic new era, laying a new foundation for understanding, protecting, and developing the brain.

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