



# Characterizing a highly excited and sustained brain response activity during gaming: P300-CE

Leisi Pei<sup>a,b</sup>, C. Shawn Green<sup>c</sup>, and Guang Ouyang<sup>b,1</sup>

Edited by Terrence Sejnowski, Salk Institute for Biological Studies, La Jolla, CA; received January 27, 2025; accepted June 20, 2025

Inspired by the high engagement and sustained behavioral excitement observed in video game players, we hypothesized that distinct brain activity patterns occur during gaming compared to a generic nongame setting. Using electroencephalography (EEG), we characterized the brain's response to critical in-game events, focusing on the response magnitude and adaptation. Data from a large participant cohort (n = 140 for game tasks, n = 200 for nongame tasks) revealed a clear, definite, and consistent temporospatial structure of brain response patterns triggered by critical in-game events. Most notably, this response displayed unusually large magnitudes and a lack of adaptation over repeated exposures—markedly different from the observed neural responses to typical events in lab-based tasks (e.g., regarding novelty, unexpected events or errors). The identification of this distinctive response component in gaming contexts may inspire further research into fundamental cognitive systems, such as motivation, reward, emotional engagement, and their dynamic interplay in gaming environments.

P300-CE | brain excitability | brain and game | event-related potential (ERP) | EEG

One distinct feature of games, especially video games, is that players can engage in them for extended periods without getting bored. This phenomenon is not common, as individuals typically grow tired of repetitive activities, an effect which is mirrored in adaptation of underlying neural signals. Specifically, adaptation manifests as a transition from high excitation and attention during early stimulus exposures to a gradually weakened response over repeated exposures. Such adaptation occurs extensively across different levels of the neural system (1-4). The robustness of the brain's adaptation to a wide variety of stimuli and the fact that games can sustain engagement despite this tendency suggest that games possess unique elements or mechanics that counteract neural adaptation, maintaining player excitement. Evolutionarily, we would expect nonadaptation phenomenon for stimuli that directly signal survival threats like pain (5). However, studying such potent stimuli ethically in a laboratory setting is challenging: Mild stimuli often lack ecological validity, while inducing genuinely threatening levels is unethical. Therefore, investigating everyday scenarios—including gaming—that elicit strong, nonadapting neural responses across repeated exposures even without direct survival implications holds significant research value.

Building on this rationale, we investigated potential neural signatures underlying the sustained excitability observed in players of video games (especially fast-paced game genres). We first hypothesized the existence of a unique brain activity mode that is nondissipative during gameplay. We further proposed that this special activity mode can be characterized by distinct neural response patterns to critical events during gaming. In engaging games—whether video games or sports—such events are strategically interspersed throughout the course of gameplay and are often tied to decisive outcomes (e.g., a shot in a ball game). These events are cognitively and emotionally salient and are expected to be capable of eliciting strong and sustained neural responses. For instance, in a first-person shooter game, even within a virtual setting, being shot at constitutes a high-stakes event that would consistently excite the players across instances.

In cognitive neuroscience, characterizing the brain's response to specific events—typically discrete stimuli—is a fundamental approach to studying brain functions. Yet, prolonged and potentially nonadapting neural responses across repeated exposures to discrete events have not been clearly documented or characterized in the literature; instead, adaptation has been extensively documented (6-8). In this exploratory study, we aimed to systematically characterize the brain response patterns evoked by critical in-game events and assess their magnitude and adaptation properties in comparison to conventional laboratory tasks. We recorded EEG data from 130 participants playing the game Flappy Bird (9) and compared the stimulus-evoked response patterns with data from five typical laboratory tasks (Fig. 1) conducted by 200 participants under equivalent experimental settings and environments. We selected Flappy Bird due to its simplicity, suitability for

# **Significance**

Using electroencephalography (EEG), we compared neural responses to critical in-game events with those from conventional laboratory tasks. Our results identified a unique brain response pattern, termed P300-CE, during gameplay, characterized by unusually large magnitudes and a lack of adaptation over repeated exposure. These findings suggest that high-stakes, salient in-game events engage neural pathways resistant to adaptation, potentially linked to reward and motivation systems. This work highlights the value of gaming contexts for studying sustained neural excitation and opens broad avenues for neural cognitive research.

Author affiliations: aDepartment of Curriculum and Instruction, The Education University of Hong Kong Special administrative region, Hong Kong Special administrative regions, China; bUnit of Human Communication, Learning, and Development, Faculty of Education, The University of Hong Kong, Hong Kong Special administrative regions, China; and <sup>c</sup>Department of Psychology, University of Wisconsin-Madison, Madison, WI 53706

Author contributions: L.P. and G.O. designed research; L.P. and G.O. performed research; L.P., C.S.G., and G.O. analyzed data; C.S.G. discussion; and L.P., C.S.G., and G.O. wrote the paper.

The authors declare no competing interest.

This article is a PNAS Direct Submission.

Copyright © 2025 the Author(s). Published by PNAS. This article is distributed under Creative Commons Attribution-NonCommercial-NoDerivatives License 4.0

<sup>1</sup>To whom correspondence may be addressed. Email:

This article contains supporting information online at https://www.pnas.org/lookup/suppl/doi:10.1073/pnas. 2502135122/-/DCSupplemental.

Published July 21, 2025.

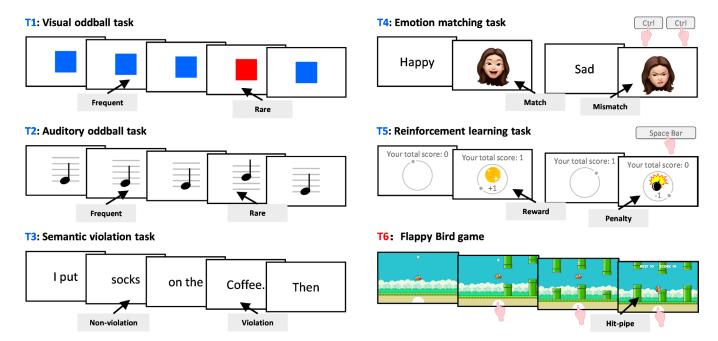


Fig. 1. Illustration of the six tasks (see details in the Materials and Methods section). T1 (Visual oddball task): participants viewed a series of squares in different colors with different frequencies and counted the number of colors. T2 (Auditory oddball task): similar to T1 but the squares were replaced by different tones with different frequencies. T3 (Semantic violation task): participants read a story segment by segment on the screen. Some segments carried semantic violations. T4 (Emotion matching task): participants viewed an emotion word followed by a cartoon facial expression. They were asked to judge whether the facial expression matched the emotion word or not. T5 (Reinforcement learning task): participants viewed a dot moving along a circle and were instructed to stop the dot at points of the circle they believed had a high probability of reward. T6 (Flappy Bird game): participants controlled a bird to navigate through as many vertical pipes as possible without hitting pipes or the ground.

experimental manipulation, representativeness of video games, and the presence of clearly identifiable, salient cognitive events.

The results showed that the brain response patterns to critical events during gameplay, as measured by event-related potentials (ERPs), displayed distinctly different characteristics compared to those observed in typical laboratory tasks, particularly in activation magnitude and sustainability. We replicated this finding using a second, custom-designed game, Space Escape, with 10 new participants. Moreover, to rule out the possibility that these effects were primarily caused by the highly dynamic and intense mental processes engaged in during video game play, we additionally administered a simple salient-event task—playing the Crocodile Dentist toy (10)—to these 10 new participants, and successfully reproduced the same neural response components observed in the two video games. These results suggest that high-stakes, critical events, condensed into rapid, impulse-like information, may be capable of eliciting neural pathways that resist adaptation. These findings may open broad avenues for research into the brain's dynamic responses to salient events, potentially involving fundamental neural circuits linked to reward, motivation, and basic drives.

### 1. Results

1.1. Descriptive Visualization and Comparison of Brain Response Patterns in Laboratory Tasks and Gameplay Contexts. We begin by presenting the cross-trial brain response patterns elicited by two types of events: 1) simple low-probability visual stimuli in a conventional oddball lab task (Fig. 1 T1) and 2) in-game critical events in the Flappy Bird game task (i.e., hitting the pipe, Fig. 1 T6) to highlight the most significant distinctions. It is important to note that this is not a quantitative comparison of specific neural effects caused by a clearly defined factor, as is commonly done in conventional cognitive research. The two tasks being compared here differ in many aspects of cognitive processing. The comparison here instead aimed to highlight the overall magnitude and cross-trial adaptation pattern during gameplay and assess its distinction from the brain response observed in a typical lab task.

Fig. 2 A and B displays the brain response patterns from the most representative electrodes across all the single trials (24 in total) of low-probability stimuli in the visual oddball task, which reveals a clear cross-trial adaptation pattern. Fig. 2 C and D displays corresponding data for the first 80 trials of recurring pipe-hitting events from the game. These single-trial results are grand averages after matching the trial order across individuals. The visualization clearly reveals an adaptation trend in the brain response pattern in the visual oddball task: Early trials show a large response to the presence of an oddball, which diminishes with repeated exposures (Fig. 2 A and B). Conversely, neural activity in response to the game failure event (pipe-hitting) in the Flappy Bird game remained high in amplitude even after 80 trials (Fig. 2 *C* and *D*).

1.2. Systematic Quantitative Comparison of the Adaptation Effects Between Game and Nongame Tasks. To more systematically compare the adaptation effects between game and nongame tasks, we aggregated data from the five typical laboratory tasks performed by the same participant cohort. Fig. 3 shows the ERP results of 11 brain response waveforms characterized by average ERPs from different events in the six tasks. The magnitude of ERPs from the game task was noticeably larger than those from the five typical laboratory tasks (T1-T5). Since each of the five typical laboratory tasks includes two event types (e.g., rare and frequent), their ERPs are plotted separately (Fig. 3). To show that the large ERP magnitude in the Flappy Bird game is not common across all types of events within the game, we plotted a comparison of the ERPs generated by the pipe-hitting and pipe-passing events in SI Appendix, Fig. S1, which showed a stark difference (i.e., not all video game events produce large-magnitude ERPs).

For a quantitative comparison between T1-T5 and the game task, we calculated ERP parameters using five metrics: 1)

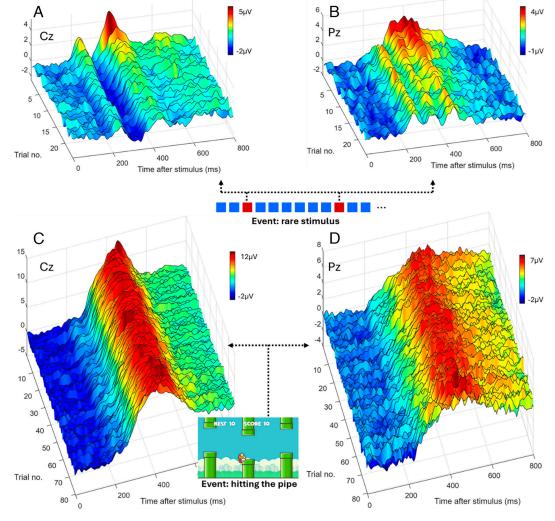


Fig. 2. Comparison of the overall brain response patterns across trials between the visual oddball task and the game task. (A and B) Grand-averaged ERPs for the 24 rare-stimulus trials in chronological order from the electrode showing the strongest late activity (Cz and Pz). (C and D) Grand-averaged ERPs for the first 80 trials of the hitting-pipe event in chronological order from the electrode showing the strongest late activity (Cz and Pz).

amplitude of waveform envelope, 2) within-participant consistency of single-trial ERPs, 3) cross-participant consistency of average ERPs, 4) signal-to-noise ratio (SNR) of ERPs, and 5) adaptation of response magnitude over trials (see detailed algorithms in *Materials and Methods*). The comparative results for the first four metrics are displayed in Fig. 4, which shows that the game task's ERP parameters stand out distinctively across all metrics.

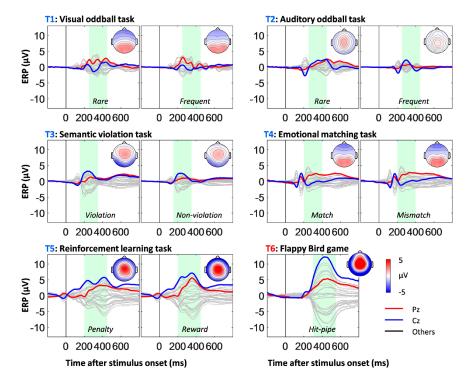
Before presenting the fifth metric, we first visualized the sustainability of brain response magnitude over trials by plotting the single-trial ERPs in chronological order (Fig. 5A, similar to Fig. 1 but now in two-dimensional planes). These single trials are again grand average results after matching the chronological trial orders across individuals. Clear adaptation effects can be observed in the majority of laboratory tasks (indicated by the arrows). In contrast, the game ERP, while showing distinctly strong activation, does not exhibit an adaptation effect (Fig. 5*A*, last panel).

To quantify the adaptation effect, we calculated the development of response magnitude across successive 30-trial blocks (Fig. 5B). Statistically, a significant reduction in neural response amplitude was found between the first and second 30-trial blocks for all lab tasks (Visual Oddball: t(199) = 3.11, P = 0.002; Auditory Oddball: t(199) = 2.87, P = 0.005; Semantic Violation: t(199) = 3.40, P < 0.001; Emotion Matching: t(147) = 7.91,

P < 0.001; Reinforcement Learning: t(199) = 3.19, P = 0.002). In contrast, the game ERP showed no decrease but an interesting increase in response magnitude [t(91) = -2.30, P = 0.024], with this high-amplitude response persisting into the third 30-trial block (Variation in degrees of freedom in the t tests was due to unequal trial numbers across participants).

1.3. Replication of In-Game Response Patterns in Two Additional Scenarios. The comparative analysis above showed that the brain's response to critical in-game events exhibits unique and distinguishable temporospatial patterns. We now term this unique response component P300-CE (P300 critical event variant), as it shares spatiotemporal characteristics with the classic P300 response—an electrophysiological signal peaking at 300 ms or later after stimulus onset (11). Here, after compensating for the 100 ms technical delay in the triggering process between Android and Python systems (Materials and Methods), the peak of the P300-CE from Flappy Bird aligned with this latency.

To further validate the association of P300-CE with high-stakes critical events, we conducted additional EEG recording from 10 new participants playing another two simple games designed to elicit salient critical events. The first one is a self-developed fast-paced video game, called Space Escape, in which participants maneuver a circle object through a field of randomly moving dots.



**Fig. 3.** Grand average ERPs time-locked to stimulus/event onset. The ERP waveforms for all electrodes are overlaid, with electrodes Pz and Cz highlighted. The scalp maps display the spatial distributions of grand average ERPs within a specific time window (indicated by green shading).

The critical event was colliding with the dots. The second game was physical, rather than a video game, namely playing the Crocodile Dentist toy (10). Here, the players press the crocodile's teeth one by one. The critical event was the crocodile toy's sudden snapping action.

The P300-CEs from the three critical event-generating tasks are shown in Fig. 6. Both the temporal and spatial patterns are consistent across the three game tasks (Fig. 6 B, F, and J). The magnitude of response remains high in the two new tasks. Note that the two new tasks were implemented in a single Python system, so there was no trigger delay, which resulted in peak time points of the P300-CE more precisely located at 300 ms. The P300-CE was reliably observed across all participants, indicating the robustness of this response across individuals. This crossparticipant robustness was consistently shown in all the three game tasks (Fig. 6 C, D, G, H, K, and L). Overall, the P300-CE component exhibits a simple spatiotemporal structure, characterized by a single hump in the time course beginning at around 180 ms and peaking at around 300 ms (also applies to the Flappy Bird

game after compensating for the trigger delay). This reproducibility across tasks and participants highlights its robustness as a neural correlate of critical event processing.

#### 2. Discussion

We reported the identification of a unique brain response pattern during gameplay, termed P300-CE, which exhibits distinctive and atypical neural characteristics. The uniqueness of P300-CE mainly lies in its high energy and nonadapting features across repeated events—a phenomenon rarely observed in laboratory tasks for basic neural cognitive research. Below we provide further clarification and discussion of these findings.

**2.1.** Inferences That Can Be Drawn by Comparing Gameplay and Lab Tasks. The most important point to clarify concerns the level at which the comparisons were made. In "standard" ERP studies, ERP waveforms are normally compared between two or more conditions (e.g., happy vs. angry faces, low- vs. high-probability stimuli) while all other factors are controlled for

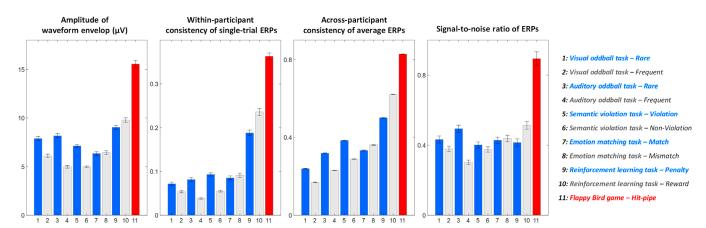


Fig. 4. Comparisons of neural response metrics representing magnitude and reliability across tasks. Bar height: mean. Error bars: SE of mean across participants.

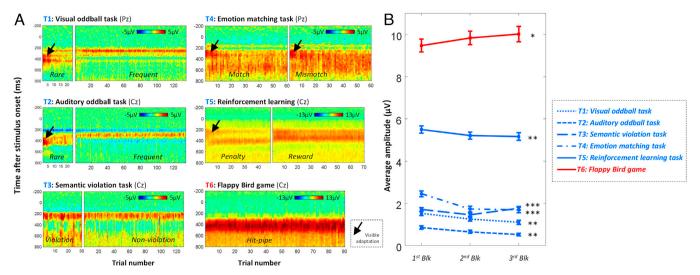


Fig. 5. Visualization and comparison of adaptation features of brain responses across different tasks. (A) Single-trial ERPs sorted chronologically. The places where clear adaptation in amplitude is visible are indicated by black arrows. (B) Comparison of mean ERP amplitude for the first, second, and third 30 trials (all conditions included and sorted chronologically) from representative electrodes and time windows (Materials and Methods) shows significant over-time reduction in lab tasks but significant increase in the game task. Note: \*P < 0.05; \*\*P < 0.01; \*\*\*P < 0.001.

equivalence. However, this study did not aim for such contrasts. Instead, this study concerned the overall output energy of brain responses elicited by discrete events and their adaptation

dynamics across repetitions. The research question was positioned at a broader level, exploring what type of (ethically acceptable) cognitive task paradigm can sustainably excite the brain. More

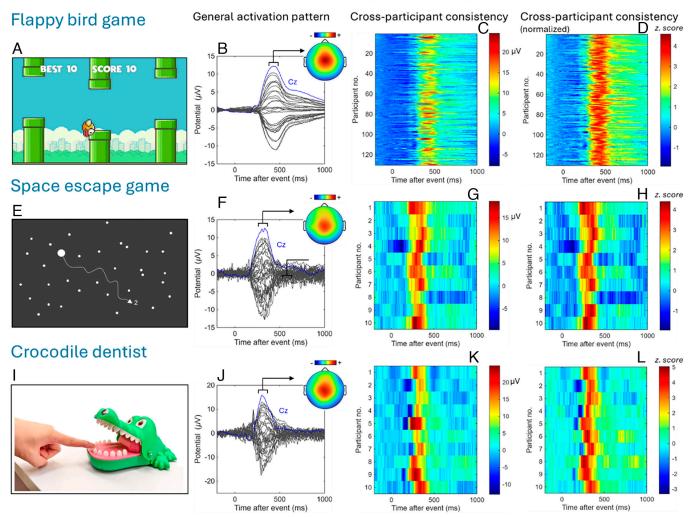


Fig. 6. Detailed characterization of P300-CE and its consistency across participants and games. (A) The Flappy Bird game. (B) Time courses of critical-event-locked ERPs for all electrodes and topographic distributions of P300-CE at the peak time window (peak latency  $\pm$  50 ms). Note that the Flappy Bird P300-CE includes a ~100-ms time course delay due to Android-Python systems communication. (C) Consistent presence of P300-CE across participants (ERPs at Cz). (D) Same as (C) but normalized to z scores for better visualization of the cross-participant consistency. (E-L): Results for the other two games.

specifically, it examines what type of stimulus input can induce high-energy, nonadapting brain responses over repeated stimulus exposures. This is not a trivial question given the brain's energyefficient principle (12-14), which leads to the typical finding that the brain response signals are weak (15) (overwhelmed by noise and spontaneous activities) and decrease over repetitions (1-4). Sustained high-energy responses require additional neural mechanisms to counteract adaptation—an effect well-documented in phenomena like pain sensitization (5, 16).

Crucially, while we demonstrated that the critical in-game events can evoke these intriguing high-energy and nonadapting brain response patterns, this study is not designed to, and cannot, pinpoint the exact factors or their interactions driving such a significant pattern shift from laboratory tasks to game tasks—a fundamental question left for future research. We propose that it is the entirety of the complex cognitive states created by the game scenarios—including situational and cognitive dynamics, player engagement, and cognitive-emotional anchoring—that enables this shift. The critical events that triggered the brain response are a point where all contextual game-player interactions are at a climax. This proposal will be discussed in more detail in the section below from a cognitive processing perspective.

2.2. The Cognitive Scenario and States Created by Games. As mentioned earlier, numerous factors or complex interactions could account for the differences between the patterns of P300-CE and typical ERPs observed in other laboratory tasks in terms of magnitude and adaptation dynamics. For example, in the Flappy Bird game, the colorful and dynamic visual field in the game scenes and the vibrant and playful game design (Fig. 1) could be major contributing factors. However, the colorless, minimalist Space Escape game helped us rule out these factors as P300-CE was intactly observed in this game. Another potential factor may lie in the need for intense cognitive processing in video games, including visual scanning, monitoring of the dynamic visual scenes for live visual motor coordination, and reward-linked active control. This is a common cognitive scenario for both the Flappy Bird and Space Escape games, as well as many fast-paced action games. Yet, the Crocodile Dentist task suggests that this may not be a strict requirement as the P300-CE was also clearly and robustly shown after the snapping event upon pressing the right tooth, which is not embedded in continuous dynamic visual motor coordination.

While the current design is not sufficient for us to pinpoint the critical factors underlying the genesis of the P300-CE, we propose a more fundamental explanation from perspectives of cognitive processes for future validation. First, it is important to note that P300-CE is not an exogenous brain response elicited by sensory input as those triggering events do not create abrupt visual input changes. This contrasts with those ERPs from the laboratory tasks, which were elicited by the sudden presentation of a stimulus from a nonexistent state. The events that generated P300-CE were more semantic and abstract in nature (e.g., signaling critical failure), rather than sensory, which makes P300-CE an endogenous response component.

From a basic cognitive perspective, the key underlying processes common across the three game scenarios can be described as follows: Players (participants) actively assembles a vast amount of cognitive resources and attention to concentrate on an impending event that 1) will occur momentarily but without precisely predictable timing or precursor event, and 2) will release information (usually binary) bearing significant cognitive relevance. In both the Flappy Bird and Space Escape, one significant cognitive implication of the event of hitting the pipe or bullet dot is the negation of the players' visuomotor coordination and control abilities. The

cognitive effort associated with reward-related control and the intense, real-time visual-motor processes, together with the game mechanics may jointly create a landscape that makes the critical events highly salient both cognitively and emotionally. Moreover, the symbolization of "death", "termination", "annihilation" in the video games may make the event more salient and relevant to players. In the Crocodile Dentist game, although the snapping down of the crocodile toy's mouth does not hurt as the teeth are made of rubber, the entire design and setting may create mental images of "biting", "tearing", "pain", "injury", and so on. Such symbolization arises from the player's understanding of and immersion in the game's narrative and mechanics (e.g., the circle hitting the moving dot symbolizes a spaceship's crashing upon hitting a space rock). Finally, these meaning-laden events, compressed into a single point of time, trigger strong neural responses.

In a nutshell, creating a high-stakes event that will be released momentarily in a simple form is proposed to be the most essential contributing factor here. Similar cognitive scenarios with high excitability and sustainability can be found across a wide spectrum of gaming and entertainment forms.

2.3. Proposed Theoretical Accounts for P300-CE from a Neural Biological Perspective. The scalp distribution of P300-CE closely resembles that of novelty-P3 [or P3a (4)], though with key differences: The novelty-P3 exhibits lower magnitude (4) and diminishes over repetitions (17). This similarity suggests that P300-CE, while being distinct from novelty-P3, may share some of its neural substrates. Novelty-P3 has been identified to be a unique neurophysiological response elicited by novel information that triggers the brain's orienting reflex (18). Its neural anatomical sources involve a distributed network supporting the brain's context monitoring and orienting responses, including frontal and temporo-parietal regions, modulated by subcortical systems (11, 19). Although the critical events in games are not inherently novel, we propose that they elicit similar responses to those generated by novelty detection through a linkage to the brain's fundamental reward and survival systems, as we elaborate below.

Events that bear strong cognitive or emotional significance are likely to impact our reward system (20–22). In skill-based games, critical events usually indicate players' success or failure in performing required actions, thereby reflecting their cognitive skills. In high-stakes situations (e.g., a decisive league match), those critical events are further tied to all benefits contingent on the outcome. The validation or invalidation of our cognitive skills is expected to activate the reward system, as these skills are evolutionarily advantageous (23, 24).

Beyond skill-approving events, various other types of discrete events can impact the cognitive system through different aspects of the reward system or primitive survival-related circuits. For instance, in a first-person shooter game, the sudden appearance of an enemy soldier at the corner may trigger the P300-CE component, not through (in)validating cognitive skill, but through symbolizing a life-threatening event (which is still powerful even in a virtual setting). Virtual settings, with appropriate designs, can effectively trigger primal neural responses despite the agent's cognitive awareness of their artificiality, much like the tension evoked by horror films. In the Crocodile Dentist game, the looming threat of being "bitten" by the crocodile toy's teeth creates visceral tension, even though the participants were fully aware that the teeth were made of rubber. If we change the setting to pressing 10 buttons on a table with a random one triggering an LED light, the P300-CE will not likely be generated (a testable hypothesis for future studies). These examples illustrate how different critical

events activate our reward system (including aversion avoidance) in different ways.

It is therefore plausible that P300-CE originates from a strong response activity in deep-brain, subcortical, and limbic system-related structures, which are evolutionarily hardwired for reward seeking and threat avoidance (25-27). These deep brain structures rapidly process reward-bearing signals and stimulate the brain's cognitive control system, preparing for subsequent actions. If correct, the wide central scalp distribution of P300-CE (Fig. 6) may partially reflect response components radiating from deep brain structures.

Future research can further validate this hypothesis by administering various tasks, both game and nongame, capable of generating the P300-CE component. The neural activity should be measured using brain imaging technologies (e.g., fMRI) to localize the relevant neural anatomical regions. A diverse array of events and paradigms could be employed to test the theory about the cognitive scenario proposed above.

The involvement of deep-brain structures may also explain the nonadapting nature of the P300-CE component. From the "new brain—old brain" perspective (28, 29), deep-brain structures are phylogenetically older than the neocortex (note that we are not adopting a simplistic binary view here). Functionally, the older and more primitive parts of the brain have hard-coded a range of response routines more directly linked to survival-critical functions (e.g., pain response) and thus exhibit rigid, hardwired reactivity (29, 30). In contrast, the newer brain regions, primarily the neocortex, are mainly responsible for analytical information processing and active learning, which displays strong adaptability and learning effects determined by their learning functions.

However, this does not imply that subcortical regions lack plasticity altogether. Learning often involves interplay between older and newer brain systems, which is manifested in behavioral changes. For instance, a highly skilled first-person shooter game player would not startle (and thus would not generate the P300-CE) upon seeing an enemy appearing at the corner if they know they are playing against beginners. However, they would still experience excitement (and thus generate P300-CE) upon seeing an enemy during competitive gameplay in a high-stakes tournament.

2.4. Implications for Basic Neural Cognitive Research. The identification of P300-CE presents significant implications for basic neural cognitive research, primarily due to its unusually large magnitude and sustainability rarely observed in typical laboratory tasks. This finding suggests the potential for developing broad research avenues by leveraging P300-CE's well-structured patterns and high signal-to-noise ratio to study the cognitive systems more effectively. Traditional cognitive tasks (e.g., visual oddball, face recognition, language processing) often encounter technical challenges due to weak signal amplitudes and high cross-trial variation caused by adaptation, leading to misrepresentation of true brain response when averaging trials (31-33). Therefore, designing tasks capable of generating P300-CE-like components hold significant research value for precisely characterizing neural processes.

Previous research has developed a variety of task paradigms that examine cognitive variables related to the game-like scenarios in the current study, such as unexpectedness, novelty, error, and reward, and their related neural signatures (e.g., novelty-P3, error-related negativity, reward positivity). However, the key P300-CE-like features have not been reported. In our task T5 (a reinforcement learning task), explicit reward and penalty signals were introduced, yet the resulting ERPs also lacked the key P300-CE features (see Figs. 3-5). This discrepancy raises an important question: Simple presentation of reward-related information in a laboratory setting may not induce the cognitive processing of reward-related information in the real world. Contextual settings, task mechanics, and stimulus characteristics, likely play essential roles in creating more realistic brain responses. To study core cognitive and affective systems (e.g., reward, drive, motivation), it may be necessary—and more informative—to create ecologically valid scenarios rather than stripped-down laboratory tasks that isolate reward signals from naturalistic contexts. While the three simple game paradigms used here do not fully replicate real-world complexity, their ability to elicit the highly atypical P300-CE response component suggests that such design evokes a qualitatively different intensity level of brain responses, more effectively tapping into fundamental cognitive-emotional processes. Well-designed game mechanics or tasks may be able to simulate semirealistic, naturalistic scenarios that effectively activate core neural systems by situating or tricking the brain into relevant states. This may be one of the factors behind the highly engaging and addictive nature of games, which is an important area of research. However, such task paradigms remain scarce in the field. Given that valuable and informative brain response signals can be generated in an ethically acceptable manner based on these paradigms, we advocate for broader application and further development of this research direction.

## 3. Materials and Methods

3.1. Participants. The EEG data for this project were collected from a total of 340 participants under the same lab setting (available for download at https:// osf.io/qp53h/). All participants were healthy Hong Kong residents with normal or corrected-to-normal vision and no history of mental illness. The data were drawn from two separate projects, a nongame project and a game project.

In the nongame project, 200 participants (mean age:  $25.14 \pm 4.51$  y; 62 male) completed a series of tasks, including a visual oddball task, an auditory oddball task, a semantic violation task, and a reinforcement learning task. Additionally, 148 of these participants (mean age:  $25.80 \pm 4.62 \text{ y}$ ; 39 males) completed an emotion matching task.

In the game project, 130 participants (mean age:  $24.69 \pm 3.31 \text{ y}$ ; 43 male) completed a Flappy Bird (9) game task. Additionally, 10 participants (mean age: 25.1 ± 6.79 y; 3 male) completed two other game tasks: Space Escape (a customized visuomotor game) and Crocodile Dentist (10) (a salient event-generating game) to further test the consistency of the game-induced brain response pattern. Written consent was obtained from each participant prior to the experiments. Both projects were approved by the Human Research Ethics Committee of The University of Hong Kong.

3.2. Experimental Design. All experiments were conducted in the same EEG laboratory using the same data acquisition system, procedures, and settings. Participants were seated in a sound-attenuated room and instructed to perform the tasks while their brain signals were recorded using a 32-channel BrainAmp DC amplifier (Brain Products, Germany). The recordings were online-referenced to electrode Fpz and digitized at a sampling rate of 1,000 Hz. The five computerbased laboratory tasks were presented using PsychoPy (34) on a desktop monitor (1,920 × 1,080 pixels, 23.8 inches, 16:9 aspect ratio). The Flappy Bird game task was implemented via a self-developed app on an Android-based tablet (HUAWEI MatePad Pro, 2,560 × 1,600 pixels, 10.8 inches, 280 PPI). The Space Escape game task was implemented using PsychoPy on the same desktop monitor. All tasks sent relevant event markers to the EEG data stream. Because the Flappy Bird game ran on an Android system, an additional time delay of approximately 80 to 100 ms occurred due to the delayed communication between the Android app in the Tablet and the Python-based trigger system in the PC caused by the additional computational cost for maintaining and updating real-time animations in the Flappy Bird game.

The tasks used in this study (Fig. 1) are described as follows. All are self-customized tasks.

- 1) Visual oddball task (6 min): Participants viewed a sequence of 160 colored squares (135 blue or red, 24 red or blue, and 1 yellow) presented randomly one by one in the center of a screen. They were instructed to count the number of colors presented. The yellow square served only a verification check and was not included in data analysis. Blue and red squares were used in data analysis, serving as the frequent and rare conditions, respectively. Each square was presented for 200 ms followed by an interstimulus interval (ISI) uniformly distributed from 1,700 to 2,700 ms.
- 2) Auditory oddball task (4 min): This task is the same as the visual oddball task except that the three colors were replaced by three tones (400 Hz, 600 Hz, and 650 Hz) each with a 200-ms duration. The ISI was uniformly distributed from 1,200 to 1,700 ms. The rare and frequent stimuli in the visual and auditory tasks were used as contrasting conditions in the data analysis.
- 3) Semantic violation task (8 min): Participants read a written story presented segment by segment on the screen. Some segments contained semantic violations, such as "rock" in "I like to eat rock." These violations occurred in 19% of the total stimuli (259 segments). Each segment was presented on the screen until being replaced by the next one. The ISI was fixed at 2,000 ms. Violated and nonviolated stimuli were used as contrasting conditions in data analysis.
- 4) Emotion matching task (3 min): Participants were shown a word ("Happy", "Sad", or "Angry") for 200 ms, followed by a cartoon facial expression that remained on the screen until a response was made. They were asked to judge if the emotion of the facial expression matched the word by pressing left (no) or right (yes) keys. The task included 120 trials, with an equal ratio of matching to nonmatching conditions. Matched and mismatched facial expressions were used as contrasting conditions in data analysis.
- 5) Reinforcement learning task (7 min): A dot moved along a circle at a constant speed of 100 degrees per second. Each point on the circle had a certain probability of yielding a reward (+1 point) or penalty (-1 point). Participants were instructed to maximize their cumulative reward by stopping the moving dot (pressing the spacebar) at points they believed had a high probability of reward. Feedback on reward or penalty was displayed immediately in the center of the screen after stopping the dot, and a new trial began once the spacebar was pressed again. The task included 120 trials, with the ERP responses to reward and penalty feedback used as contrasting conditions in data analysis.
- 6) Flappy Bird game (18 min): This game task was rebuilt on Android platform following the game rules of the original version of "Flappy Bird" released in 2013 (9). Participants controlled a bird to navigate through a series of vertical pipes with passages in between. The bird has a constant rightward horizontal speed (an illusion, as in practice the bird stays in the same horizontal position on the screen and the pipes moved leftward; see Fig. 1), and participants tapped the screen to keep the bird in the air. Each successful passage through a pipe earned the participant one point. The game ended when the bird hit a pipe or the ground, starting a new round upon tapping the screen again. All sound effects were removed. The formal session started following 2 min of practice. User events during the game were recorded and synchronized with the EEG
- system, with the bird hitting the pipe serving as the key event for EEG analysis. 7) Space Escape game (8 min): This is the first task designed to examine the consistency of brain response patterns observed in the Flappy Bird game. The key similarity between the Flappy Bird game and the Space Escape game is the presence of critical cognitive events. In the Space Escape game, participants used the four arrow keys on the keyboard to control the movement of a solid circle (radius: 12 pixels) on the screen. The screen also contained one hundred randomly wandering bullet dots (radius: 3 pixels), moving at a speed of 30 pixels per second. A target number appeared at a random position, and participants had to navigate the solid circle to the number and touch it while avoiding the moving bullet dots. Contact with a bullet dot ended the game. When the target number was reached, it disappeared, and a new number (incremented by 1) appeared at another random position for the participant to navigate to. Upon reaching a target number of 6, the difficulty level increased significantly with the addition of another 200 moving dots uniformly distributed on the screen. This heightened difficulty eventually led to the end of the game when the participant's circle collided with any of the

- dots, marking the critical event. No sound effects were added to this game. Participants played the game 12 times, generating 12 trials of EEG data that included the critical event.
- 8) Crocodile Dentist game (3 min): This is the second task designed to examine the consistency of brain response patterns observed in the Flappy Bird game. Participants played Crocodile Dentist (10), a physical toy featuring a plastic crocodile with a wide-open mouth secured by an internal lock. Pressing one of its teeth (made of rubber) released the lock, causing the mouth to snap shut and pinch participants' finger. Participants were instructed to press each tooth decisively. The session was video-recorded alongside a computer monitor displaying an evenly paced number sequence for synchronization with the EEG stream via a trigger system. The time points of the crocodile's mouth snapping were extracted from the video and used as events for ERP generation. The task consisted of 12 rounds, yielding 12 events.

#### 3.3. EEG Data Preprocessing and Analysis.

- **3.3.1. EEG data preprocessing.** EEG data preprocessing and analysis were conducted using MATLAB (MathWorks, R2021a) and EEGLAB toolbox (35). The EEG data for each task were preprocessed largely following our previous procedures (36). The specific steps in this study are as follows: 1) down-sample to 250 Hz; 2) bandpass-filter at 1 to 45 Hz; 3) interpolate EEG signals from bad electrodes identified as outliers beyond four times the median absolute deviation (MAD) across all electrodes; 4) rereference to the average. Artifact removal was conducted on the preprocessed EEG segments for each task using Independent Component Analysis (ICA) (37) and MARA toolbox (38). The probability threshold used for automatically removing non-neural artifacts in MARA was set to 0.5.
- **3.3.2.** Characterization of brain responses to key events in each task. Singletrial ERPs were obtained by extracting EEG signals surrounding the key time points in each task. The ERP epoch spanned from  $-200 \, \text{ms}$  to 1,000 ms relative to the key events, with the ( $-200 \, \text{ms}$ , 0 ms) time window used for baseline correction. Single trials from each participant and task were sorted in chronological order. Outlier trials were marked as NaN (not a number) as placeholders but were excluded from cross-participant averaging. This approach ensured the alignment of the trial order of all single trials for the grand average. The average ERPs were calculated by averaging non-NaN single trials.
- **3.3.3.** Feature comparison of ERPs across tasks. We compared eleven ERPs from the five conventional laboratory tasks and the Flappy Bird game based on the following five metrics: 1) envelope amplitude, 2) within-participant reliability of single-trial ERP, 3) cross-participant reliability of average ERP, 4) signal-to-noise ratio of single-trial ERP, and 5) adaptation of ERP across single trials. These metrics were calculated based on the electrode that displayed the strongest neural activation in each task according to the grand average ERP waveforms and scalp maps (see the electrode labels shown in Fig. 5).

Below are the algorithms for calculating each ERP feature:

- 1) Envelope amplitude: This metric assesses the amplitude of ERP, calculated as the maximum vertical range of trial-averaged ERP amplitude over the time window from -200 ms to 1,000 ms.
- 2) Within-participant reliability of single-trial ERP: This metric assesses the consistency of single-trial ERP within a single participant. For each participant, we calculated the Pearson correlations between every pair of single-trial ERPs (-200 ms to 1,000 ms) and obtained the average. This average value reflects the within-participant reliability of single-trial ERPs.
- 3) Cross-participant reliability of average ERP: This metric assesses the consistency of trial-averaged ERP across participants. We first calculated Pearson correlations of average ERPs between each pair of participants. The mean and SE of the between-pair correlations were then obtained from the entire pool. To ensure comparability across tasks, we universally used the first 20 trials to calculate the average ERP for each participant (participants with fewer than 20 trials were excluded).
- 4) Signal-to-noise ratio: This metric assesses the magnitude of ERPs relative to the background neural noise. We calculated the SNR of ERP as the ratio between the signal power and the noise power. To ensure comparability, we again only included the first 20 trials in each task. Signal power was calculated based on the SD of ERP across the time window of (0 ms, 1,000 ms), while noise power was calculated in the same way but based on the [-200 ms, 0 ms] time window.

5) Adaptation: This metric characterizes the changes in neural activation magnitude over trials and time, potentially reflecting brain adaptation. We examined the adaptation characteristics of the ERPs in both descriptive and statistical manners. Descriptively, we averaged the single-trial ERPs across participants based on matched chronological order of trials, i.e., the first trials of all participants were averaged to obtain a grand average of the first trial, and similarly for the second, third, and so on. The resulting grand average single trials were visualized in a color plot to depict adaptation effects. Statistically, we compared the amplitudes of the ERP averaged from the first 30 trials and the subsequent 30 trials by applying a paired t test. For nongame tasks, the trials for two conditions were pooled together. The amplitude was calculated from the same electrodes as above that represent the strongest global power

and from the time windows that capture the main activation of the time course (see the marked green areas in Fig. 3). Participants with fewer than 60 trials were excluded from this analysis.

Data, Materials, and Software Availability. Anonymized EEG and behavioral data have been deposited in OSF (https://osf.io/qp53h/) (39).

ACKNOWLEDGMENTS. This work was partially supported by the Hong Kong Research Grant Council General Research Fund (17609321) and Seed Fund for Basic Research from the University of Hong Kong (2202100568 and 2203100569) to G.O. Data collection was supported by Neuroscience for Education Lab Facilities at the Faculty of Education, The University of Hong Kong.

- K. Grill-Spector, R. Henson, A. Martin, Repetition and the brain: Neural models of stimulus-specific effects. Trends Cogn. Sci. 10, 14-23 (2006).
- B. Krekelberg, G. M. Boynton, R. J. van Wezel, Adaptation: From single cells to BOLD signals. Trends Neurosci. 29, 250-256 (2006).
- T. P. Reber et al., Single-neuron mechanisms of neural adaptation in the human temporal lobe. Nat. Commun. 14, 2496 (2023).
- C. Ranganath, G. Rainer, Neural mechanisms for detecting and remembering novel events. Nat. Rev. Neurosci. 4, 193-202 (2003).
- C. J. Woolf, Central sensitization: Implications for the diagnosis and treatment of pain. pain 152,
- A. Kohn, Visual adaptation: Physiology, mechanisms, and functional benefits. J. Neurophysiol. 97, 3155-3164 (2007).
- N. Ulanovsky, L. Las, I. Nelken, Processing of low-probability sounds by cortical neurons. Nat. Neurosci. 6, 391-398 (2003).
- A. I. Weber, K. Krishnamurthy, A. L. Fairhall, Coding principles in adaptation. *Annu. Rev. Vis. Sci.* **5**, 427-449 (2019).
- Flappy Bird, https://en.wikipedia.org/wiki/Flappy\_Bird. (2024).
- 10. Crocodile Dentist, https://en.wikipedia.org/wiki/Crocodile\_Dentist.(Winning Moves Games, 1990).
- J. Polich, Updating P300: An integrative theory of P3a and P3b. Clin. Neurophysiol. 118, 2128-2148 (2007).
- E. Bullmore, O. Sporns, The economy of brain network organization. Nat. Rev. Neurosci. 13, 336-349
- H. L. Li, M. C. Rossum, Energy efficient synaptic plasticity. Elife 9, e50804 (2020).
- 14. L. Yu, Y. Yu, Energy-efficient neural information processing in individual neurons and neuronal networks. J. Neurosci. Res. 95, 2253-2266 (2017).
- M. E. Raichle, D. A. Gusnard, Appraising the brain's energy budget. Proc. Natl. Acad. Sci. U.S.A. 99, 10237-10239 (2002).
- 16. P. Bessou, E. Perl, Response of cutaneous sensory units with unmyelinated fibers to noxious stimuli. J. Neurophysiol. **32**, 1025–1043 (1969).
- 17. D. Friedman, D. Nessler, J. Kulik, M. Hamberger, The brain's orienting response (novelty P3) in
- patients with unilateral temporal lobe resections. *Neuropsychologia* **49**, 3474–3483 (2011). E. N. Sokolov, Higher nervous functions: The orienting reflex. *Annu. Rev. Physiol.* **25**, 545–580 (1963).
- Y. M. Fonken, J. W. Kam, R. T. Knight, A differential role for human hippocampus in novelty and contextual processing: Implications for P300. Psychophysiology 57, e13400 (2020).
- R. A. Depue, P. F. Collins, Neurobiology of the structure of personality: Dopamine, facilitation of incentive motivation, and extraversion. Behav. Brain Sci. 22, 491-517 (1999).

- 21. J. Heckhausen, H. Heckhausen, Motivation and Action (Springer, 2018).
- 22. S. Ikemoto, J. Panksepp, The role of nucleus accumbens dopamine in motivated behavior: A unifying interpretation with special reference to reward-seeking. Brain Res. Rev. 31, 6-41 (1999).
- J. Morand-Ferron, E. F. Cole, J. L. Quinn, Studying the evolutionary ecology of cognition in the wild: A review of practical and conceptual challenges. Biol. Rev. 91, 367-389 (2016).
- M. S. Reichert, J. L. Quinn, Cognition in contests: Mechanisms, ecology, and evolution. Trends Ecol. Evol. 32, 773-785 (2017).
- S. N. Haber, B. Knutson, The reward circuit: Linking primate anatomy and human imaging.
- Neuropsychopharmacology **35**, 4–26 (2010). J. W. Papez, A proposed mechanism of emotion. Archives Neurol. Psych. **38**, 725–743 (1937).
- P. Tovote, J. P. Fadok, A. Lüthi, Neuronal circuits for fear and anxiety. Nat. Rev. Neurosci. 16, 317–331 (2015).
- W. B. Gevarter, Humans: Their brain and their freedom. J. Humanist. Psychol. 15, 79-90 (1975)
- P. D. MacLean, The Triune Brain in Evolution: Role in Paleocerebral Functions (Springer Science & Business Media, 1990).
- G. D. Stuber, Neurocircuits for motivation. Science 382, 394-398 (2023).
- I. Dinstein, D. J. Heeger, M. Behrmann, Neural variability: Friend or foe?. Trends Cogn. Sci. 19, 322-328 (2015).
- C. Pandarinath et al., Inferring single-trial neural population dynamics using sequential auto-encoders. Nat. Methods 15, 805-815 (2018).
- M. L. Seghier, C. J. Price, Interpreting and utilising intersubject variability in brain function. Trends Cogn. Sci. 22, 517-530 (2018).
- J. Peirce et al., Psychopy2: Experiments in behavior made easy. Behav. Res. Methods 51, 195-203
- A. Delorme, S. Makeig, EEGLAB: An open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. J. Neurosci. Methods 134, 9-21
- G. Ouyang, A generic neural factor linking resting-state neural dynamics and the brain's response to unexpectedness in multilevel cognition. *Cereb. Cortex* 33, 2931–2946 (2023).
  S. Makeig, A. Bell, T.-P. Jung, T. J. Sejnowski, Independent component analysis of electroencephalographic data. *Adv. Neural Info. Proc.* 5yst. 8 146–151 (1995).
- I. Winkler, S. Haufe, M. Tangermann, Automatic classification of artifactual ICA-components for artifact removal in EEG signals. Behav. Brain Funct. 7, 1-15 (2011).
- G. Ouyang, Data from "Characterizing a highly excited and sustained brain response activity during gaming: P300-CE." Open Science Framework. https://osf.io/qp53h/. Deposited 24 June 2025.