

RESEARCH ARTICLE

Nonlinear engagement of action observation network underlying action anticipation in players with different levels of expertise

Yin-Hua Chen¹ | Chih-Yen Chang^{1,2} | Shih-Kuei Huang³ | Nai-Shing Yen^{1,4} 

¹Research Center for Mind, Brain, and Learning, National Chengchi University, Taipei, Taiwan

²Department of Physical Education, National Taiwan Normal University, Taipei, Taiwan

³Department of Physical Education, Chinese Culture University, Taipei, Taiwan

⁴Department of Psychology, National Chengchi University, Taipei, Taiwan

Correspondence

Nai-Shing Yen, Department of Psychology, National Chengchi University, No. 64, Sec. 2, Zhi-Nan Rd., Wen-Shan District, Taipei 11605, Taiwan.
Email: nsy@nccu.edu.tw

Present address

Yin-Hua Chen, Graduate Institute of Athletics and Coaching Science, National Taiwan Sport University, Taoyuan, Taiwan

Funding information

Ministry of Science and Technology, Taiwan, Grant/Award Number: MOST104-2420-H-004-005-MY3

Abstract

The goal of this study was to reconcile inconsistency of neural engagement underlying action anticipation between experts and nonexperts, as well as between correct and incorrect anticipations. Therefore, we asked novice, intermediate, and skilled baseball batters (N, IB, and SB) to anticipate their swing decisions in response to pitching videos of a strike or ball, using functional magnetic resonance imaging. Behavioral results confirmed the effect of expertise that is generally shown in a linear fashion. Imaging results instead revealed a nonlinear relationship between expertise level and the evoked response amplitude of nodes within the action observation network. The relationship was best captured by an inverted U-shaped quadratic response profile across the three groups such that IB exhibited higher activation than did both SB and N. These empirical findings extend the framework of predictive coding as well as of neural efficiency in anticipating the action of others, and they might be associated with the underlying process to interpret the goal of the observed action and prepare one's own response. Furthermore, the right anterior cerebellum showed different levels of activation for correct and incorrect anticipations in all groups, adding novel evidence of its subtle involvement in anticipation processes irrespective of expertise status.

KEYWORDS

action observation network, baseball, cerebellum, inferior parietal sulcus, neural efficiency, perceptual anticipation, predictive coding

1 | INTRODUCTION

In sports, players are required to perceive and act in response to the rapid actions of others (an opposing player or a teammate) within hundreds of milliseconds. To shorten the intrinsic delay between sensory transduction and muscular contraction, players must anticipate the result of the observed action. For example, baseball batters have to

predict whether a pitch thrown by the pitcher will cross the home plate in the strike zone or not (as a strike or a ball) for deciding whether to initiate a swing or not. The ability to make predictions based on partial or advanced sources of information from the stimulus, such as an observed action, has been referred to as perceptual anticipation (Poulton, 1957). Skilled players demonstrate superior perceptual ability to anticipate the action of other players earlier and

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more accurately than their less skilled counterparts (for reviews, see Davids, Williams, & Williams, 2005; Muller & Abernethy, 2012). For example, skilled baseball batters showed higher percentages of appropriate swings than novices when they were asked to respond to a pitch that was interrupted before the ball crossed the home plate (Ranganathan & Carlton, 2007). Similarly, previous work from our laboratory found that even in the case of perceptually judging whether to swing or not (without performing a swinging action) in response to a video showing incomplete pitching sequences and ball trajectories, skilled batters could more sensitively discriminate when to swing at strikes over balls than intermediate batters (Chen, Lee, Lu, Huang, & Yen, 2017). These findings suggest that skilled batters can extract and utilize crucial information from the actions of the pitcher along with the early ball flight trajectory to determine swing decisions, whereas less skilled batters have to wait until they can visualize the entire pitching sequence with longer ball trajectories. Such differences between experts and novices have been attributed to the fact that skilled players have encountered the observed action more frequently. Consequently, the greater visual/perceptual experience likely makes them more proficient in detecting relevant cues that specify the outcome of the observed action in order to respond accurately and in time, a concept referred to as the perceptual experience hypothesis (Abernethy & Zawi, 2007; Williams, Davids, & Williams, 1999). In contrast, the motor experience hypothesis suggests that the more experienced the observer, the more accurate the perception of the same action performed by another person (Aglioti, Cesari, Romani, & Urgesi, 2008; Urgesi, Savonitto, Fabbro, & Aglioti, 2012). This is because perception and production of an action are intrinsically linked to common codes and reciprocally induce each other (Prinz, 1997; Schutz-Bosbach & Prinz, 2007). Given that the majority of existing studies investigating players in tennis, badminton, and basketball indicate that the capacity of performing the observed action indeed stems from expertise, the motor experience hypothesis seems highly plausible and straightforward. However, in the case of baseball, for batters anticipating the result of a pitching action, the perceptual experience hypothesis might be more applicable (Chen et al., 2017).

Neuroimaging and neurophysiology studies have identified that the action observation network (AON) plays a key role in anticipating the result of an observed action (for reviews, see Smith, 2016; Abreu, Candidi, & Aglioti, 2017; Bishop & Wright, 2018; Karlinsky, Zentgraf, & Hodges, 2017). AON is a bilateral network involving frontal, parietal, and occipital-temporal regions; it is activated when watching others in action (for a review, see Caspers, Zilles, Laird, & Eickhoff, 2010). It includes the inferior frontal gyrus (IFG, Brodmann area [BA] 44/45), premotor cortex (PMC, BA 6), supplementary motor area (SMA, BA 6), primary somatosensory cortex (BA 1/2), superior parietal lobule (SPL, area 7A), intraparietal sulcus (IPS, area HIP3), rostral inferior parietal lobule (IPL, area PFT/PFop), posterior middle temporal gyrus/superior temporal sulcus (pMTG/pSTS) at the transition to visual area V5, and fusiform gyrus (FFG). Of these, the IFG/vPMC, IPS/IPL, and pMTG/pSTS are considered the most important nodes within the AON. The former two regions show so-called mirror properties; they are activated both while executing an action and observing others executing

the same action, implying that an observed action is processed in the same or similar way as it is produced (Cross, Hamilton, Kraemer, Kelley, & Grafton, 2009; di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Keysers, 2009; Rizzolatti & Craighero, 2004; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996; for a review, see Molenberghs, Cunnington, & Mattingley, 2012). In contrast, the pMTG/pSTS is also activated while observing an action in point-light displays, such as biological motion, implying that an observed action can be processed from its structural or kinematic information (Grossman et al., 2000; Grossman, Jardine, & Pyles, 2010; Herrington, Nymberg, & Schultz, 2011; Pelphrey, Morris, Michelich, Allison, & McCarthy, 2005; Saygin, 2007).

Despite this body of evidence, over half of the existing functional magnetic resonance imaging (fMRI) studies are yet to implicate a particular region within the AON as being involved in the specific capabilities of expert or novice players (Bishop & Wright, 2018; Smith, 2016). One possible reason could be that, in sports psychology research, no unified criteria for defining players as experts and novices has been identified (Swann, Moran, & Piggott, 2015). Players defined as experts range from local/country amateurs to professional/international players, across studies (Bishop & Wright, 2018; Smith, 2016), and nonexperts have been considered to be local/country amateurs in some studies and individuals lacking any related experience in others. Thus, the reported differences between experts and nonexperts have been obtained by contrasting professional players to intermediate players (Balsler et al., 2014) or professional players to individuals without any experience (Abreu et al., 2012; Wright, Bishop, Jackson, & Abernethy, 2011). If the evoked brain activation does not change as a linear function of expertise level (higher the expertise level, greater or lower the brain activation), but as a nonlinear function, then experts might exhibit different (greater or lower brain) activation than nonexperts depending on the classification of players (Abreu et al., 2012; Balsler et al., 2014; Balsler, Lorey, Pilgramm, Stark, et al., 2014; Bishop, Wright, Jackson, & Abernethy, 2013; Wimshurst, Sowden, & Wright, 2016; Wright et al., 2011; Wright, Bishop, Jackson, & Abernethy, 2010; Wright & Jackson, 2007; Wu et al., 2013). In fact, Wright and colleagues conducted some of the earliest fMRI studies to investigate the neural engagement of action anticipation in players, and importantly, they applied a three-group design that could potentially test the hypothesis of a nonlinear trend between brain activation and expertise level (Wright et al., 2010, 2011; Wright, Bishop, Jackson, & Abernethy, 2013). However, their results did not appear to support the hypothesis. It could possibly be due to an unbalanced sample size across groups and a low number of experts ($n = 8, 13,$ and 16 for experts, intermediates, and novices, respectively, in the 2010 study; $n = 8$ for all of the three groups in the 2011 study). Moreover, the comparison only between players (i.e., experts and intermediates) and nonplayers (Wright et al., 2011) and the lack of comparison between experts and novices (Wright et al., 2013) did not fully take advantage of the three-group design to capture dynamic changes in neural engagement across different expertise levels. The use of a block design was also detrimental to the study as it is less sensitive in detecting specific underlying processes, as compared to an event-related design, although block design was a commonly used experimental paradigm in

early fMRI studies (Wright et al., 2010, 2011, 2013). Finally, the use of region-of-interest (ROI) analysis instead of whole-brain analysis might also have contributed to the interpretation of the results (Wright et al., 2010).

Another small but growing body of literature proposes that the relationship between the AON response amplitude and action familiarity is not necessarily linear, as suggested by direct matching amount (AON activation increases as familiarity increases; Buccino et al., 2004; Calvo-Merino, Glaser, Grezes, Passingham, & Haggard, 2005; Calvo-Merino, Grezes, Glaser, Passingham, & Haggard, 2006; Gallese & Goldman, 1998; Rizzolatti, Fogassi, & Gallese, 2001; Urgesi et al., 2012; Wolpert, Doya, & Kawato, 2003). Instead, it is nonlinear in nature as suggested by predictive coding account (e.g., Kilner, Friston, & Frith, 2007a, 2007b). Predictive coding posits that the brain actively predicts upcoming sensory input (e.g., observed kinematics) based on empirical Bayes inference, rather than passively registering it. Given prior expectations of the goal/intention of the observed person, the observer's own motor systems are used, particularly the IFG/vPMC and IPS/IPL, to generate models of performing the same action to predict the observed action kinematics. The comparison of predicted with observed kinematics, processed in the pMTG/pSTS, generates prediction errors. These prediction errors are used to update representations of the observed motor commands and inferred goals. The AON functions to minimize these prediction errors through recurrent or reciprocal interactions between all levels of cortical hierarchy. Then, the most likely cause of the observed action is inferred at all levels (intention, goal, motor, and kinematic). This framework is best captured by a U-shaped quadratic response profile, with high AON activation when observing a novel action, which decreases and reaches a nadir when observing a moderately familiar action, and increases again when the observed action is highly familiar (Cross et al., 2012; Gardner, Aglinskis, & Cross, 2017; Liew, Sheng, Margetis, & Aziz-Zadeh, 2013). The interpretation is that when observing a novel action versus a moderately familiar action, predictions are lacking and thus do not match the observed kinematics. This will result in higher prediction errors with greater AON responses due to increased reciprocal interactions among AON regions. In contrast, when observing a highly familiar action, observers can have exact predictions, and any small deviations from the predictions amplify the AON responses if the observed kinematics do not exactly match the predicted consequences.

Gardner et al. (2017) further adjusted the U-shaped model concerning the situation when the action familiarity continues to increase. Intriguingly, AON activation continues to decrease as familiarity and experience accrue as effects of neural efficiency. The concept of neural efficiency was originally suggested to describe the economy of recruiting frontal brain regions and inter-regional connectivity while performing cognitive tasks in bright versus ordinary individuals (for a review, see Neubauer & Fink, 2009). It is considered to represent more efficient cortical functioning and a strengthening of essential couplings, as well as a pruning of unnecessary couplings based on reduced utilization of resources and improvement in information processing. As compared to nonathletes, elite athletes exhibit neural

efficiency in the SMA, left middle frontal gyrus (MFG), and left cerebellum when performing simple visuospatial tasks (e.g., multiple target pursuit, go/no-go task; Bernardi et al., 2013; Guo, Li, & Yu, 2017), and in sensorimotor areas while planning, executing, or judging domain-specific actions (Babiloni et al., 2009, 2010; Del Percio et al., 2008; Del Percio et al., 2009; Milton, Solodkin, Hlustik, & Small, 2007; Naito & Hirose, 2014).

By combining the concepts of predictive coding and neural efficiency, the nonlinear model proposed by Gardner et al. (2017) is best supported by a cubic regression model with the AON response reducing, increasing, and then reducing again as familiarity of the observed action increases. Specifically, the finding was probed from a short-term (3 days) practice program using action observation and action execution tasks (Gardner et al., 2017). Its potential application to neural engagement of action anticipation associated with longer-term experiences remains unknown. We explored it by examining the neural engagement underlying action anticipation in players who had different levels of familiarity with an observed action. To this end, we recruited novice, intermediate, and skilled baseball batters to anticipate their swing decisions in response to observed pitching actions while undergoing fMRI scanning. It would be best to test this model with four groups by adding a group of individuals without any baseball-playing experiences as a control group who would engage greater AON activity as compared to novice and skilled players. However, this was not practically possible because individuals without baseball-playing experiences cannot really visualize how the pitch is thrown until the ball is close to home plate, and thus they can only make guesses when performing the task.

Furthermore, regarding the neural underpinnings of correct versus incorrect action anticipations in players of varying skill levels, previous studies have reported inconsistent results (Abreu et al., 2012; Balsler, Lorey, Pilgramm, Naumann, et al., 2014; Balsler, Lorey, Pilgramm, Stark, et al., 2014; Wu et al., 2013). For example, Abreu et al. (2012) reported that both skilled and novice basketball players exhibit higher activation for correct anticipations than for incorrect anticipations in the left precentral and postcentral gyri, left putamen, and right cerebellum. They also reported that certain regions were exclusively activated in skilled players (bilateral posterior insular cortices) and novices (medial orbital gyrus). However, the group comparisons did not provide statistically significant results (Abreu et al., 2012). Wu et al. (2013) also reported that correct action anticipation evoked higher activation than did incorrect action anticipation; however, the activation occurred in different regions in expert players and novices (left IFG for expert basketball players and right IPL for novices). The inconsistency between these studies could also potentially be because the actions to be anticipated were not presented at natural speeds but in slow motion (Abreu et al., 2012; Wu et al., 2013). More importantly, in these studies, the anticipation tasks were typically too easy for expert players, and thus, there were only few occurrences of incorrect anticipations, which weakened the results (Abreu et al., 2012; Balsler, Lorey, Pilgramm, Naumann, et al., 2014; Balsler, Lorey, Pilgramm, Stark, et al., 2014; Wu et al., 2013). To tackle these issues, we increased the task difficulty by showing pitching sequences

with only very early ball flights (first 100 ms after ball release) at actual speeds, as done in our previous study (Chen et al., 2017).

In summary, in an attempt to reconcile the inconsistent findings of neural engagement underlying action anticipation in sports between experts and nonexperts, as well as between correct and incorrect anticipations, we asked novice, intermediate, and skilled baseball batters to anticipate their swing decisions while undergoing event-related fMRI scanning. The anticipation task was designed to be very difficult even to skilled batters, with incomplete pitching sequences shown along with early ball flight, in order to obtain sufficient numbers of incorrect anticipation from skilled batters as well. We expected to replicate previous behavioral findings that players with higher levels of expertise showing higher accuracy, shorter response times, and higher sensitivity in discriminating when to swing at strikes over balls (Chen et al., 2017; Paull & Glencross, 1997; Ranganathan & Carlton, 2007). The three-group study design allowed us to test whether the evoked neural underpinnings within the AON would exhibit a nonlinear pattern as a function of expertise level, as reflected by their familiarity with pitching action. AON activation would be lowest for novices, increasing in intermediates due to more reciprocal interactions among AON regions to minimize the prediction errors, and then decreasing in skilled batters due to efficiency. Regarding correct and incorrect anticipations, we speculated that participants would differentially evoke bilateral sensorimotor areas (precentral and postcentral gyri) and right cerebellum by exhibiting higher or lower activations. The anticipation might also interact with the expertise effect such that batters of different skill levels would exhibit higher activation in various regions due to different underlying processes.

2 | MATERIALS AND METHODS

2.1 | Participants

We recruited 18 skilled batters (SBs; mean age = 20.6 ± 1.7 years, height = 177.8 ± 6.0 cm, weight = 78.5 ± 8.8 kg, baseball-playing experience = 9.6 ± 2.5 years, training duration per week = 19.4 ± 4.3 h) from highly ranked Taiwanese university baseball teams, 16 age-matched intermediate batters (IBs, mean age = 23.1 ± 1.5 years, height = 172.9 ± 5.8 cm, weight = 66.9 ± 11.4 kg, baseball-playing experience = 3.9 ± 1.2 years, training duration per week = 5.6 ± 2.3 hr) from baseball teams of different university departments, and 16 novice batters (mean age = 21.2 ± 2.1 years, height = 173.0 ± 6.0 cm, weight = 68.4 ± 8.8 kg, baseball-playing experience = 0.4 ± 0.3 years, training duration per week = 4.1 ± 2.9 hr). The three groups were significantly different in terms of years of baseball-playing experience ($F_{(2, 49)} = 139.789$, $p < .001$, $\eta_p^2 = 0.851$; p values $< .001$ for all pairwise comparisons) and training duration per week ($F_{(2, 49)} = 116.857$, $p < .001$, $\eta_p^2 = 0.827$; p values $< .001$ for all pairwise comparisons, except for the one between IBs and novices, $p = .521$). Most of the SB participants ever participated in international competitions and they were still active in participating competitions at the time of

experiment. None of them retired. Whereas the IB and novice participants had little and no experience of formal competitions (at most twice per annum in departmental competitions within their own universities), respectively. All participants were right-handed males of approximately 175 cm height, and thus, had similar strike zones. Generally, all participants had poor experience of pitching. Some SBs had training in both batting and pitching during high school years, but reported that they had not pitched for 1–2 years prior to the experiment as they had chosen to specialize in batting. None of the participants had specific experience in other sports with the exception of one IB participant who played football for recreational purposes. They did not have any neurological disorders or contraindications to MRI. Prior to participation, all participants provided written informed consent in accordance with the procedures that were approved by the research ethics committee of the National Taiwan University and were in accordance with the 1964 Helsinki declaration and its later amendments or comparable ethical standards. Participants were reimbursed for their participation after completing the experiment.

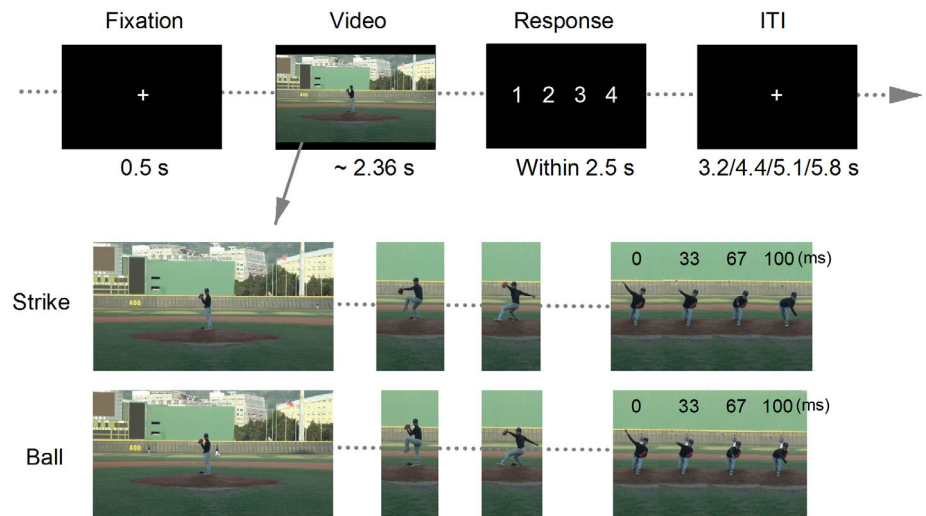
2.2 | Stimuli

We used the same stimuli as those in our previous study (Chen et al., 2017). The stimuli were color video clips of incomplete sequences of a right-handed model pitcher throwing a strike or a ball (Figure 1). We used only those videos that showed the early ball flight period of the pitching action of the model player; the videos stopped at 0, 33, 67, and 100 ms after ball release, based on the previous finding that the perceptual anticipation of SB and IB participants could be separately identified with videos of these lengths (Chen et al., 2017). The variations in video length were used to create more variable stimuli, but were not used as experimental manipulations. Overall, 144 video clips of pitches were presented (2 model pitchers \times 2 types of pitch \times 9 pitches \times 4 video lengths). Each video clip was presented once. In addition, using the same video camera setting, we filmed an additional four video clips of each model pitcher while warming up the shoulders and neck with small movements on the pitcher's mound. These videos served as control videos; they did not involve action anticipation processes but provided similar visual inputs to those of the pitch videos. They were edited to have similar lengths to those of the pitch videos and presented twice in the experiment, yielding 16 control video presentations (2 model pitchers \times 4 videos \times 2 repetitions). In total, 160 video clips were presented as experimental stimuli. The average length of the video clips was 2.36 s (standard deviation = 0.41 s).

2.3 | Task

In each trial, after viewing the video of a pitcher throwing a strike or a ball, the participants were asked to decide whether they would swing the bat or not at the pitch by pressing one of three buttons to signal the response of "swing," "no swing," or "I don't know" (uncertain). The optimal decisions would be "to swing at strikes" and "not to swing at

FIGURE 1 Timeline of trial and example of experimental video of a model pitcher throwing a strike or ball with the ball trajectory interrupted within 100 ms after ball release. The frames were zoomed in and cropped for demonstration, barring the initial frames



balls". The participants were asked to make their decision on each pitch as if the match were in a tie with a critical situation (full count of two strikes and three balls, two players out, and the bases loaded in the last inning) to maximize the importance of the decision. After viewing a control video, the participants had to press another button. The four response buttons were marked as 1, 2, 3, and 4 under the right index, middle, ring, and little fingers of the participant, respectively, and the assignment of button numbers to answers was counterbalanced across participants. Participants had to give a response within 2.5 s; otherwise, the trial was skipped and regarded as an error trial.

2.4 | Procedure

As in our previous study (Chen et al., 2017), we showed complete video sequences of the pitches (nine strikes and nine balls) from each model pitcher to the participants before testing. This was performed to familiarize the participants with the strike zone (judged on site by a skilled catcher) for each model pitcher and with the scene filmed by the video camera. We then explained the task to the participants and allowed them 10 practice trials with feedback on accuracy to familiarize them with the task. After a safety briefing, safety screening, and consent form completion, participants were taken to the scanner. The participants lay supine with their heads held still in a coil. They were first scanned at rest for 6 min, lying awake with their eyes open and relaxing their minds without thinking about anything in particular. The participants were then asked to perform the task while undergoing functional scanning. In each trial, the participants were presented with a fixation cross for 0.5 s, followed by a video clip. After the video clip was terminated, the participants were required to respond within 2.5 s. The jittered inter-trial interval was 3.2, 4.4, 5.1s, or 5.8 s (Figure 1). The video clips of the two model pitchers were tested in separate blocks, each composed of two runs. The order of the blocks and runs within each block were counterbalanced across participants.

The trials within each run were presented in random order. The participants could take a short break between runs to avoid fatigue or tedium. After the functional scans, the participants underwent structural scans with their eyes closed, including 8 min of diffusion-tensor imaging (DTI) and 6 min of T1-weighted imaging, followed by a second resting-state scan for 6 min. The resting-state functional data and DTI data were not included in this study. The total duration of the experiment was approximately 75 min depending on the response time (RT) of the participant. The experimental program was written using E-Prime 2.0 (Psychology Software Tools Inc., Sharpsburg, PA, USA).

2.5 | Data acquisition

Behavioral data, including the response and RT, were recorded with an MR-compatible button box. Imaging data were collected with a 3 T scanner (Skyra, Siemens Medical Solutions, Erlangen, Germany) equipped with a 64-channel head coil. A T2*-weighted gradient echo-planar imaging sequence was used to acquire functional images, with slice thickness = 3 mm, repetition time (TR) = 2000 ms, echo time (TE) = 25 ms, flip angle = 90°, with 41 axial slices acquired in ascending interleaved order, on a 64 × 64 matrix in a 216 × 216 mm field of view (FOV). A magnetization-prepared rapid gradient-echo sequence was used to acquire T1-weighted anatomical images, with slice thickness = 1 mm, TR = 2,530 ms, TE = 3.03 ms, inversion time = 1,100 ms, flip angle = 7°, 192 sagittal slices, on a 256 × 256 matrix in a 256 × 256 mm FOV.

2.6 | Behavioral data analysis

We calculated the rates of correct, incorrect, and uncertain decisions by dividing the number of the corresponding trials by the total number of trials for each participant in each experimental condition.

Correct decisions included cases of swinging at strikes and not swinging at balls. Incorrect decisions included cases of not swinging at strikes and swinging at balls. Uncertain decisions were cases of not knowing whether or not to swing. We then compared the rates of correct, incorrect, and uncertain decisions, as well the corresponding RTs, with two sets of three separate two-way (3 groups \times 2 swing decisions) mixed design analyses of variances (ANOVAs), with group as the between-participants factor and swing decision as the within-participants factor. We performed one sample *t*-test for each group to confirm whether their correct decisions for strikes and balls, respectively, were significantly higher than the 33% chance level. Furthermore, for perceptual sensitivity, we calculated *d'* by subtracting *z* scores of the false-alarm rate (decision to swing at balls) from *z* scores of the hit rate (decision to swing at strikes) for each participant and compared the three groups using one-way ANOVA. SPSS Statistics 21.0 (IBM Corp., Armonk, NY) was used for statistical analysis with the alpha value set at .05. Effect sizes were calculated using partial eta-squared values (η_p^2) for ANOVAs and Cohen's *d* for *t*-tests. Bonferroni's correction was used for posthoc multiple comparisons.

2.7 | Imaging data analyses

MRI data processing and statistical analyses were carried out with statistical parametric mapping software (SPM8, <http://www.fil.ion.ucl.ac.uk/spm>) implemented in MATLAB R2016b (MathWorks, Inc., Natick, MA). Functional images were slice time corrected, realigned, and then co-registered to the participant's segmented gray matter image. The images were then normalized to the Montreal Neurological Institute (MNI) standard space and spatially smoothed with an 8 mm full width at half maximum Gaussian kernel. We performed statistical analysis at both individual and group levels using a general linear model (GLM) at each voxel across the whole brain. For individual data, we modeled the action anticipation processes from images of videos with up to seven event types depending on the response of the participant (i.e., swinging at strikes, not swinging at strikes, being uncertain with regard to swinging at strikes, swinging at balls, not swinging at balls, being uncertain with regard to swinging at balls, and the response to control videos) by specifying the onsets and durations of the videos. We also modeled the potentially involved processes when the participant was presented with four response choices (following the video clip) and motor component when the participant pressed the button, along with six parameters of realignment, as regressors of no interest. All regressors were then convolved with a canonical haemodynamic response function (HRF). Contrast images between the four main event types (swinging at strikes, not swinging at strikes, swinging at balls, and not swinging at balls) and the baseline (response for control videos) were then generated for each participant and fed into a three-way (2 types of pitch \times 2 responses \times 3 groups) full factorial design using random-effects analysis as group-level analysis. The type of pitch and response were within-participants factors and group was the between-participants factor. We examined all the main effects and interaction effects. Specifically, the interaction between type of

pitch and response was used to test the differences between correct and incorrect decisions because decisions of swinging at strikes and not swinging at balls were considered correct decisions, whereas decisions of swinging at balls and not swinging at strikes were considered incorrect decisions. The main effects of response and type of pitch, as well as other two-way or three-way interactions, were not the focus of this study; nevertheless, the results have been presented in Supporting Information for completeness. The statistical maps of all the analyses were constructed with a voxel-wise intensity threshold of $p < .001$ (uncorrected) with a spatial extent threshold of $p < .01$, based on Monte Carlo simulations using AlphaSim. Activations were anatomically localized with the Automated Anatomical Labeling (AAL, Tzourio-Mazoyer et al., 2002), BA, and probabilistic cytoarchitectonic maps using the SPM Anatomy Toolbox (Version 2.2b; Eickhoff et al., 2005, 2007).

To test whether the evoked brain activation of the three groups would be linear or nonlinear as a function of expertise level, we used the MarsBar tool (<http://marsbar.sourceforge.net/>) to extract the beta value from each resultant significant cluster as an ROI for each participant and fitted the data to the years of baseball-playing experience for each participant with a linear regression and a second-order quadratic polynomial, respectively (Chang, Chen, & Yen, 2018; Gardner et al., 2017; Mattavelli, Andrews, Asghar, Towler, & Young, 2012). The goodness of the fitting for the two models for each cluster was compared with the values of adjusted R^2 , Akaike Information Criterion (AIC), as well as Bayesian Information Criterion (BIC).

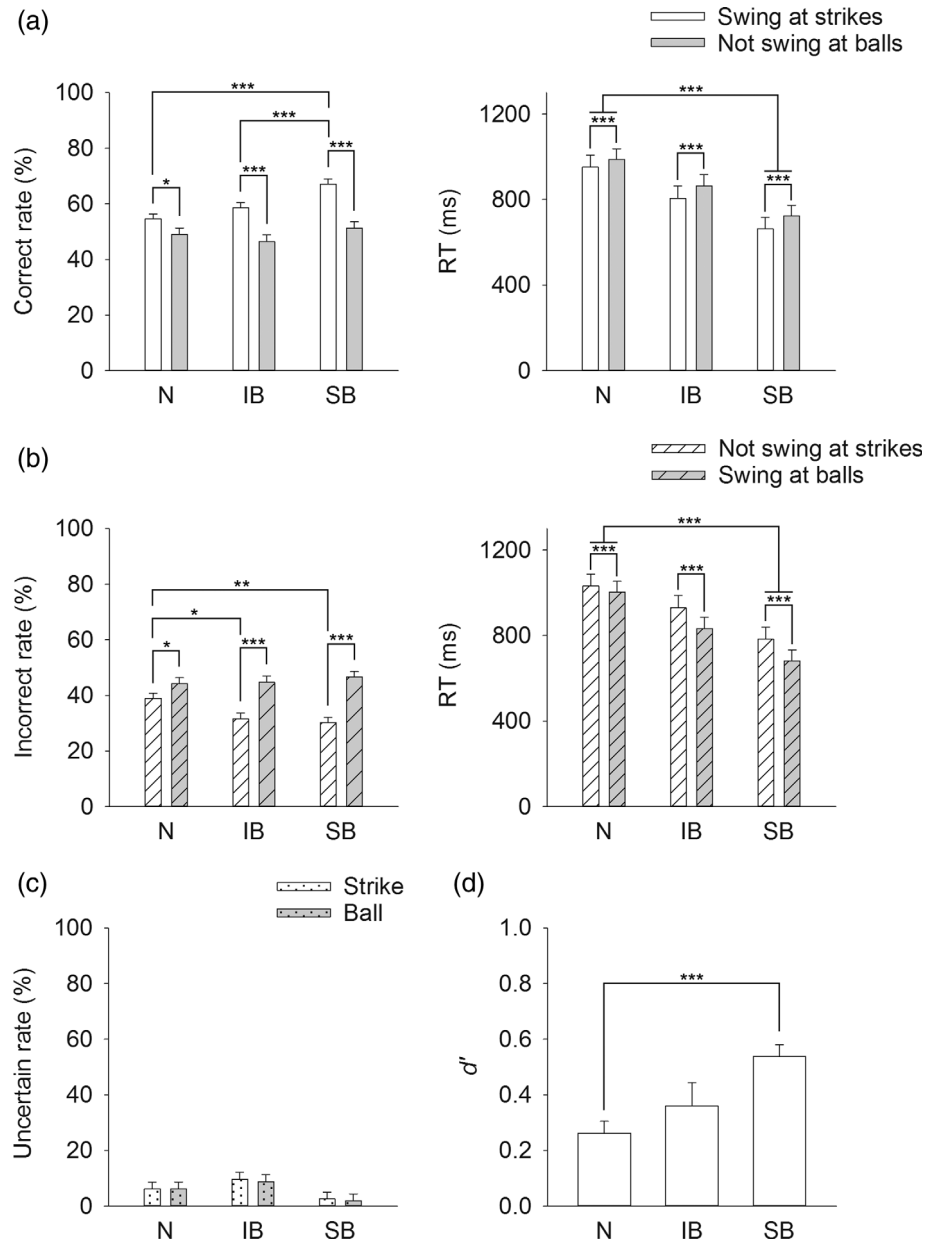
3 | RESULTS

3.1 | Behavioral results

3.1.1 | Rate of correct decisions

As shown in Figure 2a, ANOVA detected a significant main effect of group ($F_{(2, 49)} = 6.132$, $p < .005$, $\eta_p^2 = 0.220$), with SBs exhibiting a higher rate than both IBs and novices ($ps < .05$; mean values of 59.2, 52.5, and 51.7% for SBs, IBs and novices, respectively; no differences between IBs and novices, $p = 1.000$). The main effect of swing decision also reached significance levels ($F_{(1, 49)} = 60.321$, $p < .001$, $\eta_p^2 = 0.552$), with all players showing a higher rate of decision to swing at strikes (60.1%) than to not swing at balls (48.8%). The interaction effect was also significant ($F_{(2, 49)} = 4.562$, $p < .05$, $\eta_p^2 = 0.157$). Posthoc comparisons indicated that for the decision to swing at strikes, SBs exhibited a higher rate than both IBs and novices ($ps < .005$; mean values of 67.2, 58.6, and 54.5% for the three groups, respectively; no differences between IBs and novices, $p = .347$). Whereas for the decision to not swing at balls, there were no differences among the three groups ($ps > .488$; mean values of 51.2, 46.4, and 48.9% for the three groups, respectively). Moreover, all groups showed higher rates of decision to swing at strikes as compared to the decision to not swing at balls ($ps < .027$). Importantly, all of these correct decisions, irrespective of strikes or balls,

FIGURE 2 Mean rate and/or response time of (a) correct, (b) incorrect, (c) uncertain swing decisions on strikes and balls, and (d) perceptual sensitivity in discriminating when to swing at strikes over balls for the three groups of batters



were made above the chance level for all groups (p s < .001; Cohen's d values >3.5986).

3.1.2 | RT of correct decisions

ANOVA detected a significant main effect of group ($F_{(2, 49)} = 7.212$, $p < .005$, $\eta_p^2 = .227$), with SBs achieving a shorter mean RT than novices ($p < .001$; mean values of 692, 834, and 970 ms for SBs, IBs, and novices, respectively; no differences for other pairwise comparisons, p s > .195). There was also a significant main effect of swing decision ($F_{(2, 49)} = 11.677$, $p < .001$, $\eta_p^2 = 0.192$); all players achieved a shorter RT for decisions to swing at strikes (807 ms) than the decision to not swing at balls (857 ms). The interaction was not significant ($F_{(2, 49)} = 0.304$, $p = .739$, $\eta_p^2 = 0.012$; Figure 2a).

3.1.3 | Rate of incorrect decisions

As shown in Figure 2b, ANOVA detected a significant main effect of swing decision ($F_{(1, 49)} = 57.890$, $p < .001$, $\eta_p^2 = 0.542$); all players exhibited a higher rate of decisions to swing at balls (45.1%) than to not swing at strikes (33.6%). The main effect of group was not significant ($F_{(2, 49)} = 1.644$, $p = .200$, $\eta_p^2 = 0.064$; mean values of 38.3%, 38.1%, and 41.6% for SBs, IBs, and novices, respectively). Importantly, there was a significant interaction effect ($F_{(2, 49)} = 4.733$, $p = .05$, $\eta_p^2 = 0.162$). Posthoc comparisons indicated that for the decision to not swing at strikes, both SBs and IBs exhibited lower rates than novices (p s < .05; mean values of 30.2%, 31.6%, and 39.0% for the three groups, respectively). Whereas for the decision to swing at balls, there were no differences among the three groups (p s = 1.000; mean values of 44.3%, 44.7%, and 46.5% for the three groups, respectively).

Moreover, all groups showed higher rates for decisions to swing at balls than for decisions to not swing at strikes ($p < .05$).

3.1.4 | RT of incorrect decisions

ANOVA detected a significant main effect of group ($F_{(2, 49)} = 7.736$, $p < .001$, $\eta_p^2 = 0.240$), with SBs achieving shorter RTs than novices ($p < .001$; mean values of 732, 882, and 1,017 ms for SBs, IBs, and novices, respectively; no differences for other pairwise comparisons, $p > .154$). There was also a significant main effect of swing decision ($F_{(1, 49)} = 22.235$, $p < .001$, $\eta_p^2 = 0.312$); all players achieved shorter RTs for decisions to swing at balls (839 ms) than to not swing at strikes (915 ms). The interaction ($F_{(2, 49)} = 2.180$, $p = .124$, $\eta_p^2 = 0.082$) was not significant (Figure 2b).

3.1.5 | Rate of uncertain decisions

The SB participants exhibited a lower rate of uncertain decisions than did IB and novice participants (mean values of 2.3%, 9.2%, and 6.4% for SBs, IBs, and novices, respectively); however, the group differences were not significant ($F_{(2, 42)} = 2.046$, $p = .140$, $\eta_p^2 = 0.077$). The main effects of pitch result ($F_{(1, 49)} = 0.904$, $p = .346$, $\eta_p^2 = 0.018$) and interaction ($F_{(2, 49)} = 1.012$, $p = .371$, $\eta_p^2 = 0.040$) were not significant (Figure 2c). Only five, seven, and seven participants of the SBs, IBs, and novices, respectively, had RT data for uncertain decisions, and therefore, we did not perform statistical analysis for this variable.

3.1.6 | Perceptual sensitivity in discriminating when to swing at strikes over balls

The effect of group was significant ($F_{(2, 49)} = 6.015$, $p < .005$, $\eta_p^2 = 0.197$). Posthoc comparisons indicated that SBs showed a higher sensitivity than novices ($p < .005$; mean values of 0.538, 0.360, and 0.263 for SBs, IBs, and novices, respectively), but there were no differences for the other pairwise comparisons ($p > .111$) (Figure 2d).

3.2 | Imaging results

Three SBs and two novices were not included in the imaging analysis due to excessive head motion (their overall translation was >3 mm). As in the aforementioned behavioral results, the pattern of the statistics comparing the 15 SBs, 16 IBs and 16 novices for different swing decisions remained unchanged (for details see Supporting Information). Trials in which participants did not respond within 2.5 s were considered error trials and discarded from the analysis. The average number of discarded trials for each of the three groups was 1.00, 1.06, and 1.31, respectively.

3.2.1 | SB \cap IB \cap novices

We first performed a conjunction analysis of the three groups to examine which areas were recruited for action anticipation irrespective of the expertise level. Results revealed that all three groups engaged nodes of AON across both hemispheres, including the dorsal PMC, SMA, insula, IPS extending to SPL, and pMTG/pSTS. Moreover, the right MFG extending to IFG, and the left inferior occipital gyrus (IOG) extending to calcarine sulcus were also involved (Figure 3a and Table 1).

3.2.2 | Effect of group

As indicated in Figure 3b, four clusters were identified to be significantly associated with the level of expertise, including bilateral dorsal PMC, left IPS extending upward to SPL, and left pMTG/pSTS extending downward to inferior temporal gyrus (Table 1). In all of the four clusters, IBs exhibited higher activation than did SBs and novices. In addition to demonstrating group differences with a categorical approach, we further conducted regression analyses on the activation levels of each cluster using years of baseball-playing experience for each participant as a continuous variable to test whether the trend could be best approximated with a linear or a nonlinear (i.e., quadratic regression) model. For the left PMC, the activation level could be significantly predicted by both regression models ($p < .05$). Whereas for the right PMC and the left IPS/SPL, only the quadratic regression model was significant ($p < .01$). For the left pMTG/pSTS, neither regression models was significant (p values of .108 and .166 for linear and quadratic regression models, respectively). Moreover, a higher value of adjusted R^2 , and lowers value of both AIC and BIC, were found for the quadratic regression model compared to the linear regression model for all clusters, except for the left pMTG/pSTS (for details see Table 2).

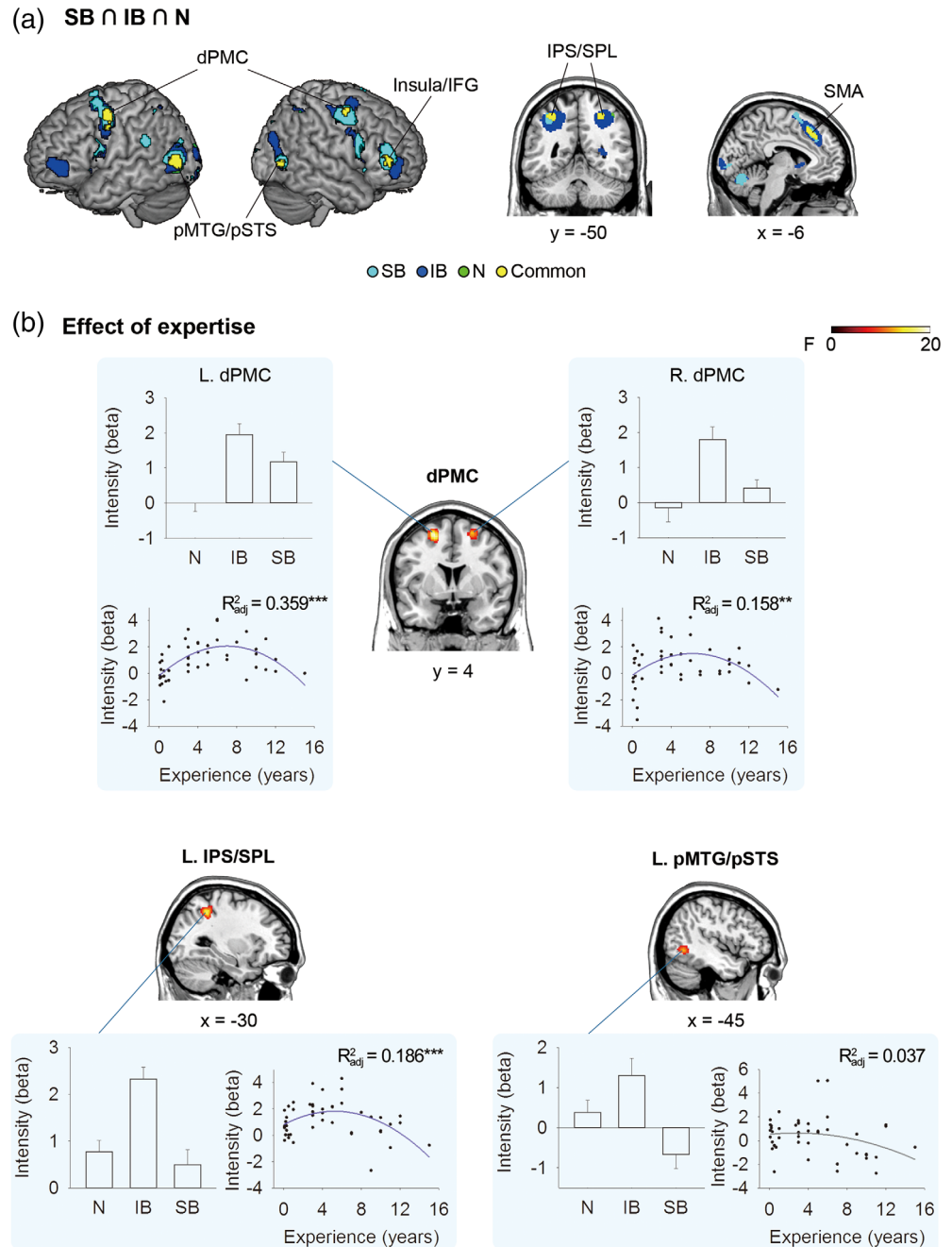
3.2.3 | Interaction of type of pitch and response (i.e., the effect of decisions: correct $>$ incorrect decisions)

We analyzed the effect of the decisions in terms of correct versus incorrect decisions. One cluster within the right anterior cerebellum (Lobule 6) that slightly extended upward to the FFG was identified to be sensitive to the interaction effect. Particularly, the significance was from a more negative activation for incorrect decisions than for correct decisions (correct $>$ incorrect decisions in case of negative values; Figure 4 and Table 1). The inverse contrast (incorrect $>$ correct decisions) did not yield any significant clusters.

4 | DISCUSSION

While expert players have demonstrated their superior capacity of action anticipation in comparison to their less-skilled counterparts

FIGURE 3 (a) Brain regions that were constantly engaged during action anticipation in all the three groups of batters. (b) Brain regions that showed the influence of expertise on action anticipation, including the bilateral dorsal premotor cortices (dPMC), left intraparietal sulcus extending to superior parietal lobule (IPS/SPL), and left posterior middle temporal gyrus/superior temporal sulcus (pMTG/pSTS). The activation intensity of the bilateral dPMC and left IPS/SPL could be fit well to the baseball-playing experience of players in quadratic regression models. R^2_{adj} , adjusted R-squared value; ** $p < .01$, *** $p < .005$



behaviorally, whether and how this capacity is underpinned by specific neural substrates remains a hotly debated topic (Bishop & Wright, 2018; Smith, 2016). To tackle this issue, baseball batters of three different expertise levels were examined when they anticipated the swing decision in response to observed pitching actions during fMRI scanning. With this three-group design, we could more subtly examine which brain regions were engaged to a greater or lesser extent in certain groups, helping us reconcile the inconsistency in differences between experts and nonexperts cited in literature. Importantly, we were able to track the dynamic changes of brain responses as a function of expertise level that were best fit by a linear or

nonlinear model. The behavioral data confirmed the effect of expertise that is generally seen in a linear fashion. The higher the expertise level, better the anticipation performance. In contrast, the imaging data indicated a nonlinear relationship, with an inverted-U shape, between the activity of the engaged AON nodes and expertise level such that moderate baseball-playing experience evoked stronger brain activity than did relatively lower and greater experiences. Such results inform both on the framework of predictive coding and the notion of neural efficiency. The right anterior cerebellum responded differently to correct and wrong anticipations, indicating its subtle involvement in the underlying processes of action anticipation.

TABLE 1 Brain regions that were consistently or differentially engaged during action anticipation in skilled batters (SB), intermediate batters (IB), and novices (N); and brain regions that responded differently to correct and incorrect decisions

Brain region	BA	Peak MNI			Cluster size (voxels)	Peak F or T value
		X	Y	Z		
SB ∩ IB ∩ N						
L. pMOG/pMTG/pSTS (hOc4la/hOc5)	37/19/39	-48	-70	6	257	5.52
R. Insula	47	30	24	-2	144	5.44
R. IPS (hIP3)/SPL (7A/7PC)	7	26	-54	54	87	4.75
L. Precentral gyrus (dPMC)	6	-42	-4	50	224	4.75
R. pMTG/pSTS (hOc4la/hOc5)	37	48	-66	0	89	4.45
L. Insula	47	-28	28	0	50	4.27
L. IPS (hIP3)	7	-32	-50	50	53	4.25
L. Calcarine/IOG (hOc3v, hOc1, hOc2)	17	-16	-94	-8	173	4.20
B. mSFG/L. SMA	6/8	-6	26	44	179	4.14
R. MFG/IFG (triangular portion)	46	44	40	4	107	4.01
R. MFG (dPMC)	6	44	-2	56	46	3.76
Effect of group						
L. IPS (hIP3)/SPL (5 L)	7	-24	-50	48	220	22.62
L. SFG/MFG (dPMC)	6	-22	6	58	194	20.77
R. SFG (dPMC)	6	22	2	60	100	13.91
L. pMTG/pSTS/pITG (FG4, hOc5)	37	-46	-60	-6	128	13.22
Effect of decision (correct > incorrect decisions)						
R. Cerebellum (VI)/ FFG (FG1, FG2, FG3, FG4)		32	-54	-22	58	3.99

Note: Significant clusters were determined using the voxel-wise height threshold of $p < .001$ uncorrected with multiple comparison correction at $p < .01$ using a Monte Carlo-determined cluster extent. Abbreviations: B, Bilateral hemispheres; BA, Brodmann area; dPMC, dorsal premotor cortex; FFG, fusiform gyrus; IFG, inferior frontal gyrus; IOG, inferior occipital gyrus; IPS, intraparietal sulcus; ITG, inferior temporal gyrus; L, left hemisphere; MFG, middle frontal gyrus; MNI, Montreal Neurological Institute; mSFG, medial superior frontal gyrus; pMOG, posterior middle occipital gyrus; pMTG, posterior middle temporal gyrus; pSTS, posterior superior temporal sulcus; R, right hemisphere; SMA, supplementary motor area; SPL, superior parietal lobule.

TABLE 2 Quadratic and linear regression models that fit the activation intensity of brain regions to the years of baseball-playing experience in all players, and the corresponding criteria, including adjusted R^2 , Akaike Information Criterion (AIC), and Bayesian Information Criterion (BIC), to compare models

Region	Type of model	Regression	p	Adjusted R^2	AIC	BIC
L. dPMC	Quadratic	$y = -0.183 + 0.645x - 0.046x^2$.000***	0.359	9.600	15.150
	Linear	$y = 0.608 + 0.096x$.047*	0.064	26.475	30.176
R. dPMC	Quadratic	$y = -0.140 + 0.531x - 0.043x^2$.009**	0.158	36.956	42.506
	Linear	$y = 0.593 + 0.022x$.699	0 (-0.019)	44.973	48.673
L. IPS/SPL	Quadratic	$y = 0.807 + 0.388x - 0.037x^2$.004***	0.186	19.820	25.370
	Linear	$y = 1.438 - 0.050x$.302	0.002	28.462	32.162
L. pMTG/pSTS	Quadratic	$y = 0.527 + 0.083x - 0.015x^2$.166	0.037	46.342	51.892
	Linear	$y = 0.783 - 0.095x$.108	0.036	45.447	49.148

Abbreviations: dPMC, dorsal premotor cortex; IPS, intraparietal sulcus; L, left hemisphere; pMTG, posterior middle temporal gyrus; pSTS, posterior superior temporal sulcus; SPL, superior parietal lobule; R, right hemisphere.

4.1 | Perceptual anticipation ability increases as a function of expertise level

Our behavioral data demonstrate that, specifically for strikes, players generally achieved a higher accuracy and lower inaccuracy, both with shorter RTs, as the level of expertise increased. The perceptual

sensitivity in discriminating when to swing at strikes over balls also showed this trend. These results collectively reflect that perceptual anticipation ability increases as a function of expertise level (Chen et al., 2017; Paull & Glencross, 1997; Ranganathan & Carlton, 2007), and are in close agreement with previous findings of studies on many other sports (for reviews, see Davids et al., 2005; Muller &

Correct > Wrong Decisions

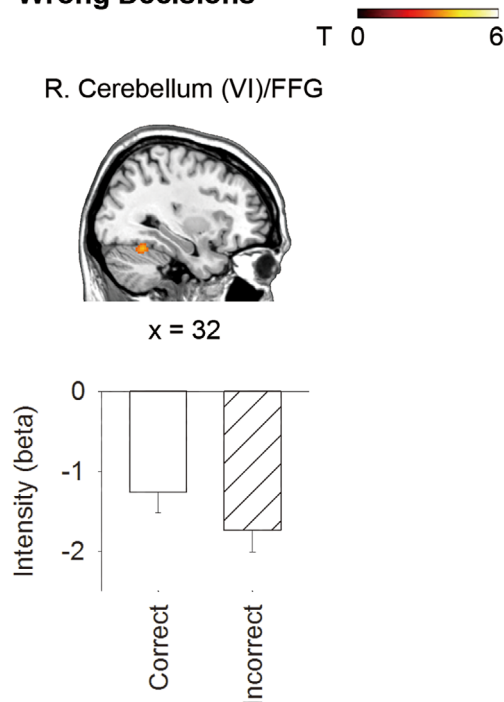


FIGURE 4 One cluster in the right anterior cerebellum (VI) that extended slightly upward to the fusiform gyrus (FFG) showed different levels of activation between correct and wrong anticipations in all three groups of batters

Abernethy, 2012; Tomeo, Cesari, Aglioti, & Urgesi, 2013). Intriguingly, the accuracy for balls was not as high as for strikes. All players exhibited a high inaccuracy for balls; they tended to swing the bat and treat the pitch as if it were a strike. This result perfectly demonstrates that our participants made their swing decisions based on the game situation set in this study (a tie game with full count, two players out, and the bases fully loaded in the last inning) (Gray, 2010) and replicated previous findings (Chen et al., 2017). Because by making this decision (i.e., swinging the bat), they could conceivably make a hit, cause an error by the opposing team, or hit a foul ball and receive another chance to swing with the pitcher (who then would be required to spend more energy throwing another pitch). This decision was also possibly made to avoid being called out on strikes, especially because pitches in this study were ambiguous for only incomplete pitching action and pitch trajectory was shown. For uncertain rates, we found that SBs had a lower rate than the other two groups, but the differences were not statistically significant, even using similar pitching videos for experimental stimuli as in our previous study (Chen et al., 2017). This could possibly be because, in this study, batters of three skill levels were compared and only very short videos (showing the pitcher's action and, at most, 100 ms of ball trajectory) were tested. Whereas in our previous study, batters of fewer (two) expertise levels were compared, and more and longer videos (showing the pitcher's action and, at most, 367 ms of ball trajectory) were tested (Chen et al., 2017).

4.2 | AON is involved in anticipating one's own response to an observed action

At the neural level, we found a clear spatial overlap of activation patterns within the AON among the three groups, replicating previous findings (Abreu et al., 2017; Bishop & Wright, 2018; Karlinsky et al., 2017; for a review, see Smith, 2016). However, in previous studies, higher neural responses in the AON, particularly in areas with mirror properties such as vPMC/IFG and IPS/IPL, in expert players were often taken as evidence of an internal simulation of the observed action, facilitating perceptual anticipation because players were motorically familiar with the observed action (Abreu et al., 2012; Balsler, Lorey, Pilgram, Naumann, et al., 2014; Balsler, Lorey, Pilgram, Stark, et al., 2014; Wu et al., 2013). The transcranial magnetic stimulation study of Aglioti et al. (2008) also supported the motor experience hypothesis by showing time-specific motor-evoked potentials during observation of erroneous basketball throws in players (motor experts) but not in coaches or sports journalists (visual/perceptual experts). Motor experience hypothesis would be a plausible conclusion had the participants of the present study been pitchers. Instead, our participants were batters who had comparatively limited ability to perform pitching actions of the same level as pitchers. Even SBs who might have had a good ability to pitch reported that they had not pitched for 1–2 years prior to the experiment. Therefore, the effect of directly simulating the observed pitching movements and possibility of evoking AON activation purely with motor experience of the observed action is likely not a significant contributor. Batters have great visual/perceptual experience of pitching actions, and are required to respond to the pitch (swing the bat) as a complementary action (Sebanz, Bekkering, & Knoblich, 2006) within a few 100 ms. The swing decisions are determined by quickly interpreting the goal of the pitching action (throwing a strike or a ball) by extracting relevant advance cues from the pitcher's movement kinematics and early ball trajectories. Therefore, the AON engagement in our batters might reflect the effect of a mixture of visual/perceptual experience with observed pitching action and the motor experience of responding to it. However, despite the poor experience with pitching, batters were still able to simulate the observed pitching movements and thus the possibility of the motor experience of the observed action in evoking the AON activity could not be totally ruled out. Moreover, whether the evoked AON activity is mainly contributed by their visual/perceptual experience of the observed action, or the motor experience of responding to it (i.e., swinging the bat) is not fully clear. Future studies should consider these two aspects by investigating pitchers and umpires due to their comparatively purer motor and visual/perceptual experience of pitching actions, respectively.

Following the framework of predictive coding (Kilner et al., 2007a, 2007b), activity in the parietal regions, particularly the IPS, represents the goal of the observed pitching action at a more abstract level, irrespective of observed kinematics (Hamilton & Grafton, 2006; Hickok, 2009, 2013; Hickok & Hauser, 2010; Kilner, 2011). The IPS is relevant in implementation of one's complementary response to an

observed action (Kokal, Gazzola, & Keysers, 2009; Newman-Norlund, van Schie, van Zuijlen, & Bekkering, 2007; Sacheli et al., 2015); disrupting this region with brain stimulation impairs performance during complementary interactions (Sacheli et al., 2015). Together with the SPL, the IPS is considered to act along the dorso-dorsal stream of the dorsal visual pathway (Binkofski & Buxbaum, 2013; Pisella, Binkofski, Lasek, Toni, & Rossetti, 2006; Rizzolatti & Matelli, 2003) and is specialized in processing structural characteristics of currently-viewed objects (e.g., shape, size, and orientation) to execute prehensile actions (for a review, see Binkofski, Klann, & Caspers, 2016). Based on these findings, activity in the IPS/SPL might be related to the underlying processes for inferring the goal of the opponent's action via visuospatial information conveyed by the ball trajectory, specifically for implementing one's own complementary action. In contrast, for the activity found in the occipital-temporal and visual regions, particularly in the pMTG/pSTS and FFG, such activity might be associated with processing of sensory input such as kinematics or any other bodily cues of the action performed by the pitcher (Grossman et al., 2000, 2010; Herrington et al., 2011; Pelphrey et al., 2005; Saygin, 2007).

Other than its mirror property, the PMC has been reported to be involved in predicting ongoing dynamic events, ranging from complex human actions to nonbiological actions such as object movements or ocean waves (Schubotz, 2007; Wolfensteller, Schubotz, & von Cramon, 2007). Together with the SMA, it has been implicated in encoding complex patterns of motor output and selecting appropriate plans to achieve desired end results (Cisek & Kalaska, 2005; Gerloff, Corwell, Chen, Hallett, & Cohen, 1997). Collectively, activity found in the PMC and SMA might be considered as results of predicting the dynamic events of either the pitcher or the ball from a more general perspective of planning complementary actions.

4.3 | Responses of AON nodes change as an inverted U-shaped function of experience

We found significant differences among the three groups with respect to the bilateral dorsal PMC, left IPS/SPL and pMTG/pSTS—all important nodes of the AON. The intensity of the evoked activation did not change linearly as a function of expertise level; instead, it exhibited an inverted U-shaped profile across the three groups such that intermediates exhibited greater activation than did both novices and experts. These results reconcile the previously inconsistent findings of higher and lower activation in experts than intermediates or novices (Abreu et al., 2012; Balsler, Lorey, Pilgramm, Naumann, et al., 2014; Balsler, Lorey, Pilgramm, Stark, et al., 2014; Bishop et al., 2013; Bishop & Wright, 2018; Wright et al., 2010, 2011; Wu et al., 2013; Xu et al., 2016; for a review, see Smith, 2016). Furthermore, by fitting the activation intensity of the brain region from each player to the corresponding baseball-playing experience, we found that in three of the four regions (except for the left pMTG/pSTS), a quadratic regression model showed better fitting than a linear one. Importantly, all criteria that we used to compare models (i.e., adjusted R^2 , AIC, and

BIC) penalize the model with more parameters. Therefore, the better fitting of the quadratic regression model compared to the linear one could not be attributed to its more parameters. These results were partially concordant with the nonlinear model proposed by Gardner et al. (2017) depicting the AON engagement (high-low-high-low) with increasing movement familiarity during action observation and execution though the completely untrained individuals were not tested (see Introduction). Our results further extend this model, while also invoking predictive coding (Kilner et al., 2007a, 2007b) and neural efficiency (Neubauer & Fink, 2009), to action anticipation associated with varying levels of expertise reflected by a mixture of visual/perceptual familiarity of the observed action and motor familiarity during the response. In other words, the framework of predictive coding is not necessarily constrained to cases where the observed action can be mapped onto one's own motor system based on same motor experience; it can be more flexibly applied to cases where the observed action is familiar based on visual/perceptual experience that is used to interpret and represent the goal of the observed action for one's complementary action. Moreover, decreased activation from intermediates to experts provides novel empirical evidence of neural efficiency in perceptual anticipation, thus extending current knowledge regarding neural efficiency in sensorimotor areas found in expert players while planning, judging, and executing domain-specific actions (Babiloni et al., 2009, 2010; Del Percio et al., 2008, 2009; Milton et al., 2007; Naito & Hirose, 2014).

Based on the framework of predictive coding (Kilner et al., 2007a, 2007b), the higher activity within the AON nodes in intermediates compared to beginners might be considered as greater reciprocal interactions that minimize prediction errors between the prediction and observed input at varying levels. At the level of movement kinematics, the pMTG/pSTS might be involved. Whereas at the level of movement goals, the IPS might be the relevant brain region. Aside from this, the PMC and IPS/SPL might also be associated with planning and prediction of complementary actions (swinging or not swinging the bat), respectively. The lower activity of these regions in the experts as compared to intermediates reflects the economy of recruiting these neural resources. Specifically, how the neural resources were used efficiently still needs further investigation. For example, whether it is the same neural computation being performed for the same amount of time but with lower intensity, or at the same intensity but with shorter lengths of the time; it could be also possible that the same neural computation is being performed with identical time and intensity but lower metabolic expenditure (Poldrack, 2015).

4.4 | The right anterior cerebellum responds differently to correct and incorrect anticipations

The other important goal of this study was to investigate the neural underpinnings of correct anticipations compared to that of incorrect anticipations. In previous studies, experts typically achieved a very high rate of accuracy (~80%) and therefore, only the correct anticipations were investigated due to scarcity of incorrect anticipations. This

did not allow for robust statistical analysis (Abreu et al., 2012; Balsler, Lorey, Pilgramm, Naumann, et al., 2014; Balsler, Lorey, Pilgramm, Stark, et al., 2014; Wu et al., 2013). Another defect of previous studies was their method of presenting the action sequences at unrealistic speeds (Abreu et al., 2012; Wu et al., 2013). We corrected these problems by increasing the task difficulty and providing very limited sequences of real pitching actions to a sufficiently high number of participants, so as to acquire a more balanced number of trials between correct and incorrect anticipations. Our results revealed that the right anterior cerebellum (Lobule VI) extending to FFG showed different levels of (de)activation for correct and incorrect anticipations, irrespective of expert status, consistent with the findings of Abreu et al. (2012) where even partial trials were analyzed. This result is also in line with the findings of Balsler, Lorey, Pilgramm, Naumann, et al. (2014), which showed that activation within the bilateral cerebellum and SPL linearly correlated with anticipation accuracy, irrespective of the expertise level. Cross, Stadler, Parkinson, Schutz-Bosbach, and Prinz (2013) also reported the involvement of the right cerebellum (VI) in anticipation processes, but not specifically for correct anticipations, in experimental participants originally lacking any prior motor experience of the observed actions and then receiving 3 day visual/perceptual training in the sequences of the observed actions. They proposed that the cerebellum organizes the temporal component of perceptual anticipation, as also seen in previous temporal spatial prediction tasks (Diedrichsen, Verstynen, Lehman, & Ivry, 2005; Dreher & Grafman, 2002; O'Reilly, Mesulam, & Nobre, 2008). While various lines of evidence indicate that the cerebellum has considerable influence on perceptual processes in addition to its long-recognized role in fine motor control (for a review, see Baumann et al., 2015), our results add novel evidence for its involvement underlying action anticipation and, more importantly, its sensitivity to successful versus unsuccessful anticipations.

4.5 | Inconsistencies in studies investigating pitch identification

Several previous studies have investigated the neural underpinning of pitch identification using fMRI by asking players to anticipate the type of pitch (fastball, curveball, or slider) after they viewed incomplete baseball trajectories (Muraskin, Sherwin, & Sajda, 2013; Ryu, Kim, Ali, Kim, & Radlo, 2015; Sherwin, Muraskin, & Sajda, 2012). However, the ball trajectories were simulated rather than thrown by a pitcher (Muraskin et al., 2013; Sherwin et al., 2012). These studies reported the involvement of areas of visual processing and motion processing, including the lingual gyrus, lateral occipital cortex (LOC), middle temporal visual area (Muraskin et al., 2013), MOG, and declive of the cerebellum (Ryu et al., 2015). Specifically, correct pitch identification was correlated with visual and subcortical motor areas (the LOC, middle temporal visual area, putamen and globus pallidus). These data indicate a link between visual identification and rapid motor responses (Muraskin et al., 2013). Incorrect pitch identification was correlated with prefrontal cortex activity, which has been implicated in prospective memory, recall, and task difficulty (Muraskin et al., 2013; Sherwin et al., 2012). The discrepancy

between the results of our study and those of previous studies might be explained by task differences and the complexity and presence of pitching action in the experimental stimuli.

5 | CONCLUSIONS

In the past decade, studies of action observation and anticipation using fMRI have provided remarkable insights into the neural plasticity of functional brain systems in expert sports players, particularly within the AON and cerebellum. Here, we further provide novel evidence of nonlinear involvement of the AON nodes, specifically the bilateral dPMC, left IPS/IPL, and pMTG/pSTS, as a function of expertise level. These empirical findings extend the framework of predictive coding as well as of neural efficiency. Moreover, the neural activation evoked by correct anticipations in contrast to that by incorrect anticipations in the right anterior cerebellum, irrespective of the batters' experience, also sheds light on our understanding of the subtle involvement of the cerebellum in the processes of action anticipation.

ACKNOWLEDGMENTS

This work was supported by the Ministry of Science and Technology, Taiwan (MOST104-2420-H-004-005-MY3). We thank the Taiwan Mind & Brain Imaging Center, supported by the Ministry of Science and Technology, Taiwan, and National Chengchi University for consultation and instrumental availability.

CONFLICT OF INTEREST

None declared.

ORCID

Nai-Shing Yen  <https://orcid.org/0000-0002-7077-7400>

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

How to cite this article: Chen Y-H, Chang C-Y, Huang S-K, Yen N-S. Nonlinear engagement of action observation network underlying action anticipation in players with different levels of expertise. *Hum Brain Mapp*. 2020;41: 5199–5214. <https://doi.org/10.1002/hbm.25186>