Predictive error processing distinguishes between relevant and irrelevant errors after visuomotor learning

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Error processing is an important aspect of learning. The detection and online correction of an error as well as error-based adaptation of subsequent movements enables humans to improve behavior. For this improvement, it is necessary to differentiate between relevant and irrelevant errors. Behavioral adaptations are only reasonable when an error is attributed to one's own behavior and therefore regarded as relevant for subsequent adjustments, whereas irrelevant errors caused by unsystematic external influences should be disregarded. Here, we ask whether error predictions as indexed by the error-related negativity (Ne/ERN) can be used to differentiate relevant and irrelevant errors in movements with a complex visuomotor mapping. Using event-related potentials, we compared the neural activation between relevant (self-induced/internal) errors and irrelevant (externally manipulated) errors in a virtual goal-oriented throwing task. Results show that the Ne/ERN responds more strongly to self-induced errors, while the feedback-related negativity (FRN) more strongly correlates with externally manipulated errors. Moreover, subsequent behavioral adjustments were larger in the relevant compared to the irrelevant error trials. We conclude that predictive processes, marked by the Ne/ERN, can subserve error attribution in naturalistic, complex visuomotor tasks like throwing.

Introduction

Imagine a biathlete shooting. The shot misses its target. Since the biathlete does not want to miss again in the next shot, it is necessary that she evaluates her shooting outcome. Trivially speaking, she needs to detect that she had made an error and attribute the error to a specific cause in order to decide whether the observed error is relevant or irrelevant. Only relevant errors would require adjustments to computations within the visuomotor system for the next shot. For instance, an observed error would be relevant only if the biathlete misperceived the situation, selected the wrong movement plan, or inadequately specified the

movement parameters. In this case, the error would be self-generated. Irrelevant errors, in response to which subsequent adjustments would not be required or even be harmful, are errors that had been caused by unsystematic variability of environmental conditions (e.g., if a sudden burst of wind had deflected the bullet), i.e., unsystematic and externally generated. Adjusting behavior to account for a singular external disturbance is thus detrimental if the external disturbance is subsequently absent or different. Hence, the visuomotor system needs to accurately estimate the relevance of perceived errors in order to derive adequate corrections.

Wei and Körding (2009) developed a relevance estimation model that computes whether an error was caused by factors within the visuomotor system or by an unsystematic disturbance in the external world. In their model, this decision is based on two factors: (a) the size of the observed error indicating that individuals tend to consider errors as irrelevant (and thus caused by unsystematic external influences) if they are exceedingly large, and (b) the way error information is integrated over time, factoring in the elapsed time since an error occurred during learning. Here, we seek to explore another aspect of assigning relevance to observed errors: the use of internal forward models that predict the sensory consequences of motor commands based on information about the current state of body and environment as well as a copy of the motor commands sent to the muscles (Shadmehr, Smith, & Krakauer, 2010; Wolpert, Diedrichsen, & Flanagan, 2011; Wolpert & Flanagan, 2001).

The concept of forward models was first considered by Helmholtz (1867). He suggested that eye position, rather than being determined by sensory signals from the eye, is predicted based on a copy of the motor command sent to the eye muscles, termed efference copy. This concept was later supported by experimental work from von Holst and Mittelstaedt (1950), and Sperry (1950). They showed that on the basis of efference copy, internal feedback (corollary discharge) is generated which can predict the sensory consequences of a movement far before the current sensory feedback is available. In addition to its effectiveness in controlling rapid movements such as saccades where peripheral feedback is too slow to affect the movement, previous research has shown that temporal and/or spatial discrepancies between internally predicted and externally registered sensory signals are used to dissociate self-generated from externally generated movements. Sato and Yasuda (2005), for instance, showed that whether individuals experience themselves as the agent behind a perceived event crucially depends on whether the perceived sensory signals from the environment conform to internally generated predictions about the consequences of an executed action.

Indeed, failures of this ability have been shown to be associated with mental disorders (Lindner, Thier, Kircher, Haarmeier, & Leube, 2005). Analogously, we hypothesize that forward model predictions can also be used to distinguish self-generated from externally generated errors, tagging the former as relevant for subsequent behavioral adjustments.

In our previous research, we analyzed event-related potentials (ERPs) during the execution of a semivirtual, goal-oriented throwing task in order to probe forward model predictions in the course of motor learning (e.g., Maurer, Maurer, & Müller, 2015). The temporal separation between movement execution (throwing) and the observation of its outcome (hitting or missing a target) allows us to separately examine two ERP components that have been related to error processing: (a) The error-related negativity (Ne/ERN; Falkenstein, Hohnsbein, Hoormann, & Blanke, 1991; Gehring, Goss, Coles, Meyer, & Donchin, 1993), which refers to a fronto-central signal with negative polarity occurring shortly after the onset of an erroneous motor action and prior to feedback about the terminal action outcome, and (b) the feedback-related negativity (FRN; Miltner, Braun, & Coles, 1997), which shares brain topography and polarity with the Ne/ERN but occurs 100–200 ms after feedback about the action outcome (Holroyd et al., 2004). According to the reinforcement theory of the error-related negativity of Holroyd and Coles (2002), the Ne/ERN is the first indicator that an action outcome will be worse than expected on the basis of *pre*-diction (comparison between intended and predicted terminal action outcome). The FRN is the first indicator that an action result is worse than expected on the basis of *post*-diction (comparison between intended and actual sensory feedback about the result modulated by prediction). The efference copy, based on which the forward model computes its prediction, comes from a so-called inverse model (Kawato, 1999; Wolpert, Miall, & Kawato, 1998). The inverse model selects motor commands that will produce a certain desired change in state or action outcome (in our biathlon example, hitting the target). Importantly, inverse and forward models need to be trained with respect to a certain task, and they learn differently (Cisek, 2005; Jordan & Rumelhart, 1992). Especially early in the learning phase, the inverse model can be inaccurate, sending out motor commands that ultimately fail to produce the desired action outcome. In addition, unsystematic fluctuations or environmental changes can affect the output. The forward model receives these wrong efferences (in form of the efference copy), and it can predict the failure to achieve the intended action outcome. Moreover, it continuously receives information and can update its prediction even after sensory information inflow to the inverse model has terminated.

Consequently, if the visuomotor system has a reliable forward model of the respective visuomotor transformation and is thus able to predict an outcome error during action execution, the system does not need to rely on a second error signal, which becomes available with the presentation of outcome feedback. On the neurophysiological level, this means that Ne/ERN and FRN should behave in a complementary manner (Holroyd & Coles, 2002). When an outcome error can be predicted, a Ne/ERN, but no FRN should emerge. In case that an error prediction is not possible or inaccurate, the FRN should indicate that an error has been detected based on the perception of the (unpredicted) actual action outcome. The latter should be the case whenever insufficient information is available for prediction, when a poor predictive forward model of the visuomotor transformation exists, or, most crucially for the present purpose, when unsystematic external influences cause the error.

There is empirical evidence that the Ne/ERN is a neural correlate of outcome error prediction in an auditory-motor mapping task (Lutz, Puorger, Cheetham, & Jancke, 2013) as well as in a throwing task (Joch, Hegele, Maurer, Müller, & Maurer, 2017; Maurer et al., 2015). With respect to the distinction between relevant (self-generated) and irrelevant (externally manipulated) errors, the prediction of an outcome error is only possible for self-generated errors because unsystematic external influences cannot be predicted. For cognitive tasks, it has been found that the Ne/ERN correlates with self-generated errors but not with external errors in an Eriksen flanker task and that external errors are followed by a FRN (Gentsch, Ullsperger, & Ullsperger, 2009; Padrao, Gonzalez-Franco, Sanchez-Vives, Slater, & Rodriguez-Fornells, 2016; Steinhauser & Kiesel, 2011). Such cognitive tasks, however, make it difficult to scrutinize the distinction between relevant and irrelevant motor errors. Errors in these tasks are related to the decision which key had to be pressed; and they are provoked by conflicting responses and temporal restrictions. Hence, consequences for the subsequent behavior after an error are not much dependent on the cause of the error. Posterror slowing is typically found as a reaction to errors in flanker tasks (e.g., Debener et al., 2005), indicating a change in response strategy towards more cautious responses (Rabbitt, 1969). However, the movement itself does not need to be adapted when committing a decision error in these tasks. This condition is different for motor errors as in the biathlete example at the beginning: To improve her shooting outcome, the biathlete needs to correct internal errors by changing movement kinematics and/or dynamics, while adjustments after unsystematic external errors would be rather detrimental. To our knowledge, there is no evidence so far indicating that

the differentiation between self-generated and externally generated errors manifests in a correlation of the Ne/ERN and FRN with learning relevant error attribution in visuomotor tasks. Earlier, we defined error relevance in relation to behavioral consequences. In other words, relevant, internal errors should be followed by subsequent behavioral adjustments, while irrelevant errors should be disregarded.

The present study sought to elucidate whether error predictions as indexed by the Ne/ERN could be used to differentiate irrelevant from relevant errors, which subsequently drive behavioral adaptation in naturalistic movements with a complex visuomotor mapping. Hence, we used a ballistic throwing task and compared self-induced (internal) errors in the throwing task with externally manipulated errors. As the external error manipulation could not be perceived by participants, external errors should not be predictable by the forward model, and thus not be correlated with a Ne/ERN. Furthermore, we expected to find a complementary behavior of Ne/ERN and FRN amplitudes in the comparison between internal and external errors. On the one hand, we assumed that the FRN should be higher in external errors since there is no prior indication of this error. Error valuation can only be accomplished by processing feedback of the terminal action outcome. In self-induced internal errors on the other hand, the FRN is expected to be smaller since the erroneous outcome had already been predicted before external feedback could have been observed. With respect to behavioral adjustments, we expected to find larger adjustments on the kinematic level after internal errors relative to external errors.

Methods and materials

Participants

We tested 21 participants (four males, 17 females) with an average age of 22 years ($SD_{age} = 2.3$). Participants were healthy and had normal or corrected-to-normal vision. All participants were right-handed and had been recruited from the student population of the Justus Liebig University Giessen. They received course credit for their participation. In addition, a total amount of 60 € was awarded to the best three participants in terms of task performance (1st place: 30 €; 2nd place: 20 €; 3rd place: 10 €). The experiment was conducted in accordance with the ethical standards of the Declaration of Helsinki. The protocol was approved by the local Ethical Review Board. Three participants had to be removed from the sample due to technical problems during data acquisition.
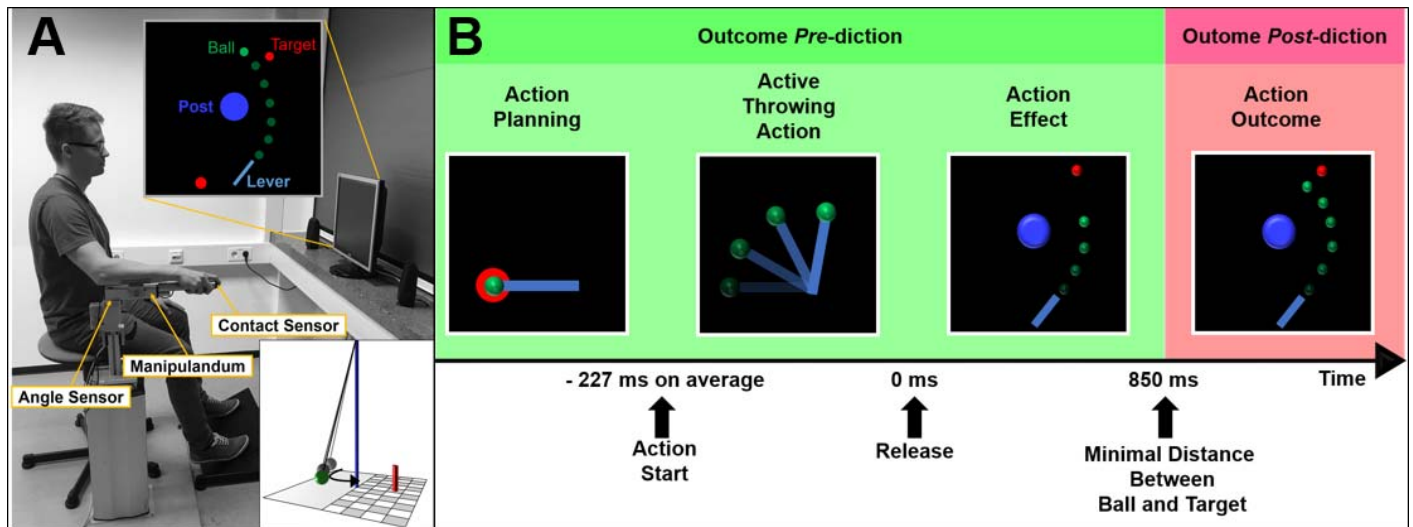
Figure 1. (A) Setup of the Skittles task. The participant uses the manipulandum to throw the green ball with a horizontal rotational movement. The throwing movement starts with the lever positioned in the red circle. The ball trajectory is depicted by a succession of green balls which resembles the static outcome feedback (see below). The insert shows the real model of the task. The depicted participant gave written informed consent for the publication of this picture. (B) Phases of a throw separated into the parts relevant for outcome *prediction* (green) and outcome *postdiction* (red). Note that the action effect, i.e., the ball travelling towards the target, was not shown to the participants during the experimental session. They saw the ball trajectory only as static feedback depiction 850 ms after ball release.

Task and performance feedback

Task and procedure

As experimental task, we used a semivirtual throwing task adapted from the British pub game Skittles. In this game, one has to toss a ball around a vertical post to which it is attached with a string with the aim to hit one or several target skittles located at the opposite side of the post. In its virtual adaptation, a TARGET circle (radius on display = 2.5 mm), the center POST (radius on display = 12.5 mm), and the BALL (radius on display = 2.5 mm) are displayed on a computer screen (size: 15-in., format: 3:4; model: AOC 919Va2, screen resolution: 1024 × 768 Pixels) from a bird's eye perspective (Figure 1A). The ball can be thrown using a metal lever, on which participants place their throwing arm. A virtual version of this lever is displayed on the screen as well. The ball is attached to the virtual lever during the throwing movement.

Participants sat on a stool placed 100 cm in front of the computer screen. The lever could be rotated within the horizontal plane around a vertical rotation axis centered on the participant's elbow joint. In order to throw the ball, participants first placed their arm on the lever and touched a contact sensor at its tip with their index finger, which automatically picked up the ball and attached it to the virtual lever. Next, they rotated the lever in a clockwise direction within the horizontal plane. The virtual lever on the screen moved analogously to the participants' arm movement. Upon lifting off the finger from the contact sensor, the virtual ball was released from the virtual lever and travelled

towards the target. The ball's trajectory was determined by the simulated physics of the task (Müller & Sternad, 2004) and described an elliptic path around the post. In the model, the relevant objects were defined as followed: POST (radius = 0.25 m; position: $x = 0.0$ m, $y = 0.0$ m), TARGET (radius = 0.05 m; position: $x = 0.8$ m, $y = 0.9$ m), BALL (radius = 0.05 m).

To prevent a rhythmic sequence of throwing, participants had to move the ball into a red start circle positioned to the left of the fixed end of the lever (corresponding with a 0° lever position in the physical model). When the ball reached the red start circle, it immediately turned yellow and, subsequently, green as soon as the lever was kept within that circle for at least one second. The green circle was used as a cue that the participants were now allowed to initiate the throwing movement at any time. Note however that participants did not start the throwing movement as a reaction to the green signal. The general task instruction was given in a standardized way at the beginning of the study. To keep up motivation throughout the whole experiment, participants were told that the best three performers with respect to target hit rates would be rewarded with 30 € for the first, 20 € for the second, and 10 € for the third place.

Each experimental session had an average duration of 90 minutes including preparation time for the EEG and task execution. Before the start of every session, participants were instructed that they could take breaks at any time during the experiment. However, most participants did not take any breaks at all, executing all 400 trials in a row.

Performance feedback

Task performance was quantified by the number of hits relative to the total number of trials (i.e., hit rate). A hit was achieved when the distance between the ball's center and the target's center was less than 10 cm in the physical model of the task. This distance was exclusively determined by release angle and velocity of the ball. Participants received feedback about their performance with respect to the action effect (ball trajectory) and with respect to the action outcome (target hits or misses). During a practice phase preceding the experimental sessions, both types of feedback were provided after each trial. In detail, participants saw the ball detaching from the lever upon release and flying towards the target in an elliptic trajectory. If the ball hit the target, a collision sound was played, the target object was knocked out of its position, and the German word for "hit" ("Treffer") was displayed in green on the computer screen. In case of an error, participants received the feedback "Unfortunately a miss" ("Leider vorbei") written in red. In addition to the dynamic ball flight, a static display of the ball's trajectory was shown isochronically to the verbal feedback (see Figure 1). The action effect (ball flight) was not provided during the experimental sessions (see Study design). Instead, only feedback about the action outcome (written message, sound signal, and static display of ball trajectory) was shown after each trial. Information about the current hit rate was provided after every 25 trials.

Study design

Participants executed the throwing task on five days (400 trials each). The first two days served as practice; the electroencephalogram (EEG) was recorded on days three to five. Pilot data indicate that the dynamic display of the ball flight towards the target is essential for learning the transformation between the horizontal arm movement and the vertical ball trajectory on the screen. However, the display also influences the neural prediction process (Joch et al., 2017). Analogous to Joch and colleagues, we initially provided dynamic information about ball flight to the participants, but faded it out during subsequent phases of the practice sessions. For the first 200 trials of the first session, participants received full visual feedback of the ball flight, i.e., from ball release until the point at which the minimum distance between ball and target was reached (100% dynamic ball flight). We then incrementally faded out this information. First, we reduced the display from 100% of the ball flight duration to 66% of the duration for 100 trials and then to 33% of the duration for the last 100 trials of that session. Thus, 66%/33% feedback of ball flight meant that the ball was

removed from the screen when it had traveled two thirds/one third of its flight duration, respectively, and only the static feedback was shown at the end (at the time of target contact or target miss). On the second day, participants started with 66% dynamic ball flight display, which was again decreased every 100 trials by 33%. As a result, they executed the last 200 trials of day two with 0% dynamic ball flight information. In the 0% condition, the ball disappeared at the moment of ball release, and participants solely received the static trajectory feedback and the result feedback about hit or error after 850 ms (average time the ball flies to the target object; see Figure 1B). The following three experimental sessions were conducted with 0% ball flight trajectory.

In order to compare the neural correlates of error prediction in self-induced and external errors, we manipulated roughly every 20th trial of sessions 3–5 that was going to be a hit to be fed back as an error. The manipulation was exclusively rendered on release velocity. Deviations from an optimal release velocity (that would result in a perfect central hit for a given release angle) were augmented by steps of 0.1 m/s until the combination of the original release angle and the new velocity caused the ball to miss the target by at least 12 cm (see ERROR criterion in Behavioral data preprocessing for EEG analysis). By manipulating release velocity, we produced external errors but kept one part of the original behavior (i.e., release angle). As a result, we compared three trial types: HIT trials, self-induced ERROR trials, and externally manipulated error trials (ERROR$_{EX}$).

After completion of the experiment, participants filled out a postexperimental questionnaire with two increasingly detailed questions about the error manipulation. In the first question, participants were asked whether they had noticed anything specific during the five sessions. Some participants reported that they thought we had moved the target position, which was not the case. The others did not report anything. The second question asked concretely for a mismatch between an expected hit and error feedback received. No participant noticed such a mismatch.

EEG data acquisition and preprocessing

We recorded EEG data and electrooculographic (EOG) data on days three to five with a 16 channel AC/DC amplifier with Ag/AgCl active scalp electrodes manufactured by Brain Products in Germany. Electrode positioning was done according to the international 10–20 system (Klem, Lüders, Jasper, & Elger, 1999) using the actiCAP electrode cap by Brain Products. Specifically, we used the electrodes F3, Fz, F4, FCz, C3, Cz, C4, P3, Pz, P4, and placed the ground

electrode on the Fpz position. EOG electrodes for measuring eye artifacts were placed above and below the right eye and on the external canthi of both eyes. We referenced data online with an electrode placed on the left mastoid. Offline rereferencing was done with average mastoids. Electrodes impedances were kept below 15 kΩ. EEG and EOG were recorded using a 500 Hz acquisition frequency.

After data acquisition, EEG and EOG data was preprocessed offline using the Brain Vision Analyzer 2.1. software. First, the signals were filtered using a Butterworth filter with a low cut-off frequency of 0.1 Hz and a high cut-off of 30 Hz. To correct for ocular artifacts, we applied the ocular correction algorithm of the Analyzer 2.1 software, which is based on the Infomax Independent Component Analysis (ICA; Makeig, Bell, Jung, & Sejonwski, 1996; Makeig, Jung, Bell, Ghahremani, & Sejonwski, 1997). To calculate the ICA components, only EEG activity around blinks was fed into the ICA algorithm. Blinks were detected by the mean slope algorithm by Gratton, Coles, and Donchin (1983). After visual inspection, the component(s) explaining more than 30% of the eye movements were removed from all other EEG activity.

After EOG correction, the signal was segmented starting 600 ms before ball release and ending 750 ms after outcome feedback (i.e., 1600 ms after ball release). A baseline correction was executed with respect to different time spans for Ne/ERN and FRN (Ne/ERN: 0–200 ms after ball release; FRN: 100 ms before feedback presentation, i.e., 750 ms–850 ms after release). Finally, each segment was manually controlled for remaining artifacts.

Behavioral data preprocessing for EEG analysis

The electrophysiological potentials of interest, the Ne/ERN and FRN, typically emerge when an incorrect action is executed. Therefore, target hits and target misses had to be separated for further analyses. To do so, the minimal distance between the center of the thrown ball and the center of the target was calculated yielding a distance (D) value. In the underlying physical model, ball and target both had a radius of 5 cm. Hence, trials with a D value greater than 10 cm were classified as misses. Trials in which the center post was hit were excluded from the analysis. Because marginal results could blend the neural signals of hits and errors, we classified only trials with $D \leq 7$ cm as HITS and trials with $D \geq 12$ cm as ERRORS. From a total of 1200 experimental trials per participant, we matched the number of HIT trials for EEG segment averaging by the number of ERROR trials, as there were more HIT than ERROR trials. In order to increase the effect size of the

difference HIT versus ERROR, we sorted the HIT trials before matching and discarded the HITs with larger distances to target center (although they were still within the 7 cm criterion). ERROR_EX trials had only been interspersed about every 20th trial. Hence, we took all ERROR_EX trials for averaging. As a result, we used on average 240 HIT and ERROR trials ($\pm$ 86.4, *range* = 91–380) and 68 ERROR_EX trials ($\pm$ 4.3, *range* = 62–77) per participant. All trials used for averaging were taken evenly from all three experimental sessions.

To confirm that participants had learned the task before EEG data recording to a point that enabled them to predict the terminal action outcome of their throws, we analyzed performance as represented by the hit rate in percent over the five sessions with an ANOVA with repeated measures.

Processing of kinematic data

To examine behavioral adaptations in response to errors, we determined changes on the kinematic level in the subsequent trial. We calculated the average absolute difference between an error trial (n) and its subsequent trial ($n + 1$) as well as between a hit trial (n) and its subsequent trial ($n + 1$) with respect to the task-relevant variables release velocity and release angle. These adjustments in release velocity and angle were averaged over all participants and compared between self-induced errors and externally manipulated errors.

Statistical analysis

For the statistical analyses, we used Mathworks MATLAB R2016a. To be able to statistically analyze the electrophysiological data, we conducted a mean amplitude analysis of the FCz segments since the amplitudes of Ne/ERN and FRN are typically highest on the FCz position (e.g., Hajcak, Holroyd, Moser, & Simons, 2005). We averaged HIT, ERROR, and ERROR_EX curves for every participant and computed difference curves between ERROR segments and HIT segments, between ERROR_EX and HIT segments, and between ERROR and ERROR_EX segments. The difference curves were then averaged over a priori set effect windows (EffW) for the Ne/ERN (200–350 ms after ball release; EffW_ERN) and the FRN (150–350 ms after feedback; EffW_FRN) to yield a mean amplitude for EffW_ERN and EffW_FRN for each participant (with reference to Joch et al., 2017, 2018; Maurer et al., 2015). The resulting mean amplitudes were tested with a one-sample *t* test using a test value of zero. Effect sizes (d) were calculated as the grand

average amplitudes divided by the standard deviations of the individual averages.

In addition, we used a Bayesian inference approach to calculate Bayes factors (*BF*) that can be interpreted as the amount of evidence for the null-hypothesis before versus after seeing the data (Verdinelli & Wasserman, 1995). Bayes factors were computed in JASP 0.8.2.0. The size of the *BF*s are interpreted according to Raftery (1995). As priors for the expected effect size, we used a Cauchy distribution as shown in the equation below.

$$f(x) = \frac{1}{\pi} \cdot \frac{\gamma}{\gamma^2 + (x - x_0)^2}$$

To adjust the location and the width of the distribution, we set $x_0 = 0$ and $\gamma = 0.7$.

Results

Behavioral results

Performance was measured as the hit rate over the five sessions. As can be seen in Figure 2A, participants improved over all five sessions, $F(2.47, 42) = 21.8$, $p < 0.001$, $\eta_p^2 = 0.56$. This result was supported by the Bayesian inference approach yielding a Bayes Factor of $BF_{10} > 100$ (corresponding to a positive evidence after Raftery, 1995). On average, participants improved from a hit rate of 48.3% in the first session to a hit rate of 73.4% in the last session. The biggest improvement (11.8%) took place in the practice phase from session 1 to session 2. In the experimental sessions (with EEG recordings), performance ranged between 66.3% and 73.4%. The improvement rate decreased with every further session, although it never clearly reached an asymptote.

Kinematic analyses showed a significant difference in corrective behavior after internal versus external errors (Figure 2B,C). Self-induced internal errors were followed by a stronger change in release velocity, $t = -8.11$, $df = 17$, $p < 0.001$, $d = 1.9$, $BF_{10} > 100$, and release angle, $t = -6.25$, $df = 17$, $p < 0.001$, $d = 1.47$, $BF_{10} > 100$, compared to externally manipulated errors. External errors did not differ from hits with respect to subsequent velocity corrections, $t = 0.67$, $df = 17$, $p = 0.51$, $d = 0.16$, $BF_{10} = 0.434$. Corrections in release angle were significantly larger in external errors compared to hits, $t = 3.77$, $df = 17$, $p = 0.002$, $d = 0.89$, $BF_{10} = 51.35$. This difference was, however, less distinct as the difference between internal and external errors: $Mean_{Ext-Hit} = 0.68°$, $Mean_{Int-Ext} = 1.5°$; $t = -2.1$, $df = 17$, $p = 0.02$ (one-tailed), $d = 0.51$, $BF_{10} = 3.14$.
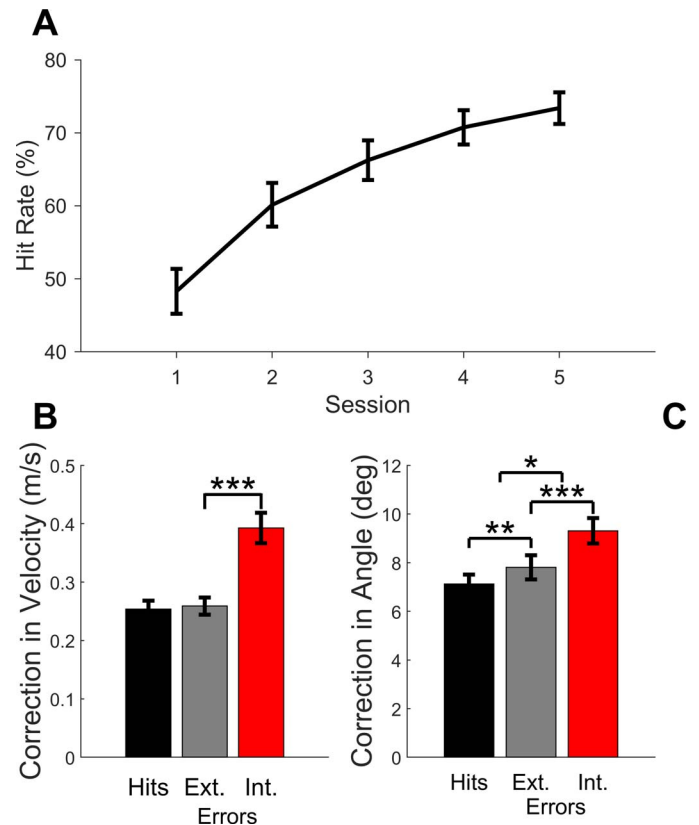

Figure 2. Top: Development of task performance in terms of hit rates over the five practice sessions. Sessions 3–5 were used for EEG recording. Bottom: Behavioral corrections after internal (red), external (gray) errors, and hits (black) quantified by the average absolute difference in velocity and angle between an error trial and the subsequent trial. Error bars represent standard error of the mean.

Electrophysiological results

Ne/ERN

Figure 3A and C depict difference waves of the three outcome categories for the Ne/ERN. After release, the curves for the HIT trials and the $ERROR_{EX}$ trials develop relatively similar, while the ERROR curve becomes more negative beginning 100 ms after release. On average, this difference is slightly offset with respect to the expected effect window $EffW_{ERN}$ 200–350 ms after release. The *t* test on mean amplitudes did nevertheless confirm the difference between ERROR and HIT: *mean difference* = −0.72 μV; $t = -1.84$, $df = 17$, $p = 0.04$ (one-tailed), $d = 0.44$. This result was also supported by the Bayesian inference approach yielding a Bayes Factor of $BF_{10} = 1.55$. The EEG curves of $ERROR_{EX}$ and HIT did not differ within $EffW_{ERN}$: *mean difference* = 0.23 μV; $t = 0.77$, $df = 17$, $p = 0.45$, $d = 0.19$, $BF_{10} = 0.31$. A descriptive illustration of these differences is also shown in Figure 4. A comparison of mean amplitudes for ERROR and $ERROR_{EX}$ with each other revealed a significant difference as well:
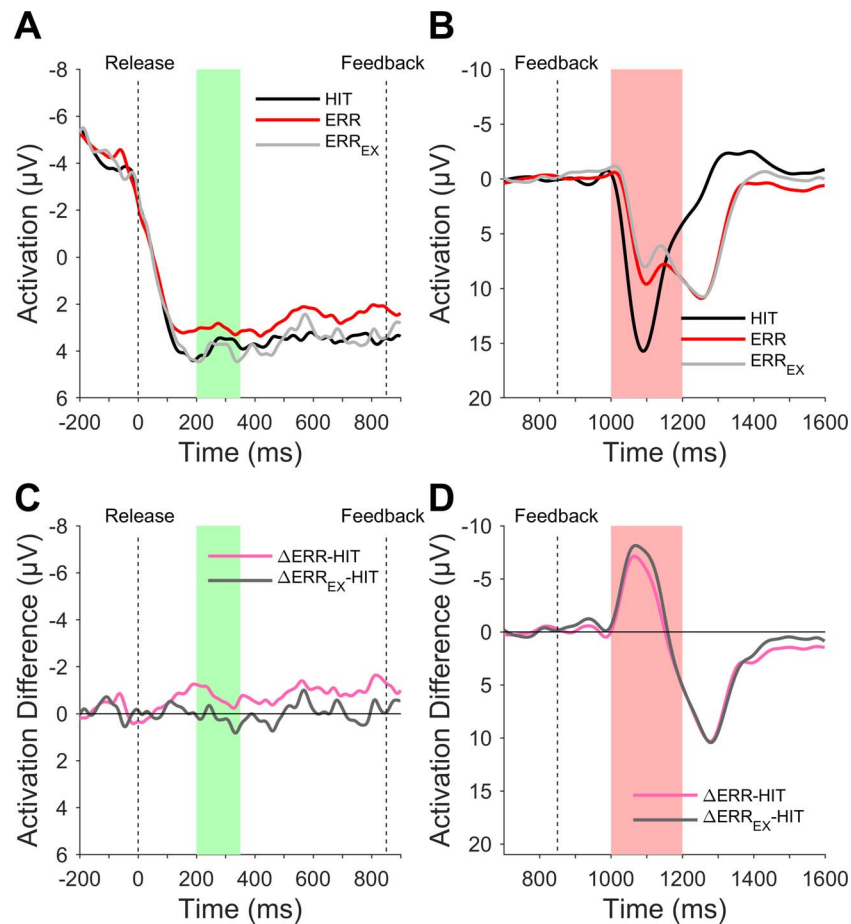
Figure 3. Grand average EEG signals with respect to error *prediction* (A) and error *postdiction* (B) for hits (HIT), self-induced errors (ERR), and externally manipulated errors (ERR$_{EX}$). The green shaded area marks the effect window EffW$_{ERN}$, 200–350 ms after ball release (0 ms). The red shaded area marks the effect window EffW$_{FRN}$, 150–350 ms after result feedback (850 ms). Difference waves between self-induced errors and hits as well as between externally manipulated errors and hits (C), (D).

mean difference $= -0.95$ µV; $t = -2.44$, $df = 17$, $p = 0.02$, $d = 0.58$, $BF_{10} = 4.7$. Thus, internal errors were correlated with a stronger Ne/ERN as hits and external errors.

FRN

Error-related signals can also be observed after the presentation of outcome feedback for both internal and external errors (see Figure 3B and D). ERROR compared to HIT trials differed significantly within EffW$_{FRN}$: *mean difference* $= -2.5$ µV; $t = -4.07$, $df = 17$, $p < 0.001$, $d = 0.96$, $BF_{10} > 100$; as did ERROR$_{EX}$ compared to HIT: *mean difference* $= -3.6$ µV; $t = -6.61$, $df = 17$, $p < 0.001$, $d = 1.56$, $BF_{10} > 100$. The amplitudes of these signals, however, were inversely related to the difference in EffW$_{ERN}$. The FRN signal was larger for ERROR$_{EX}$ trials compared to ERROR trials: *mean difference* $= -1.03$ µV; $t = 2.76$, $df = 17$, $p = 0.01$, $d = 0.65$, $BF_{10} = 4.16$.

In conclusion, the EEG curves in EffW$_{ERN}$ and EffW$_{FRN}$ exhibited complementary patterns for external and internal errors (Figure 4). The Ne/ERN amplitude was higher while the FRN amplitude was reduced in cases of self-induced (internal) errors and vice versa in trials with externally manipulated errors.

Discussion

The aim of the present study was to test whether the human visuomotor system uses predictive processes to distinguish between relevant and irrelevant performance errors in a naturalistic task with complex visuomotor mapping. To this end, we examined the effects of (internally) self-generated versus externally manipulated performance errors in a semivirtual throwing task on both the behavioral and neurophysiological level. More specifically, we hypothesized that,
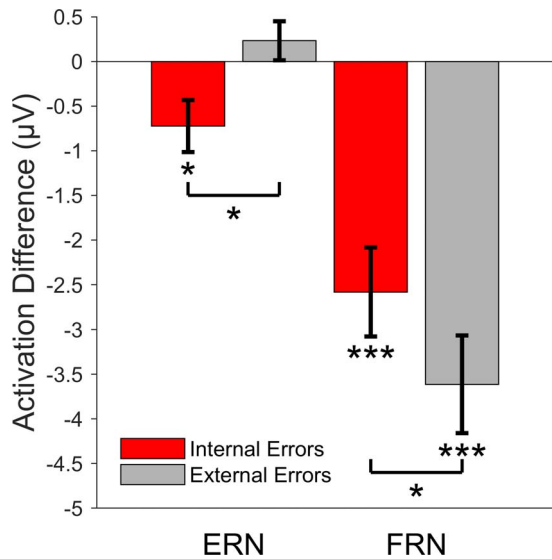
Figure 4. Comparison between the Ne/ERN and FRN for self-induced errors (internal in red; mean amplitude of the differences curves between ERROR and HIT, within $EffW_{ERN}$ and $EffW_{FRN}$ respectively) and externally manipulated errors (external in gray; mean amplitude of the differences curves between $ERROR_{EX}$ and HIT, within $EffW_{ERN}$ and $EffW_{FRN}$ respectively). Error bars represent standard errors of the mean.

on the one hand, the Ne/ERN, representing outcome error prediction, tagged self-generated errors as relevant for subsequent behavioral adjustments. Irrelevant external errors, on the other hand, were expected to emphasize *postdictive* error processing as indicated by the feedback related negativity (FRN), which should behave complementary to the *predictive* processes. We compared the ERP signals in two different time windows (corresponding to Ne/ERN and FRN) between self-induced errors and externally manipulated errors in a goal-oriented throwing task.

Error prediction correlates with internal error attribution

Results revealed a pronounced fronto-central negativity 200–350 ms after ball release (and 500 ms before outcome feedback) in trials where self-induced errors were committed relative to hits and relative to externally manipulated errors. At that time, participants could neither perceive information about the action effect (i.e., ball flight), nor the terminal action outcome (i.e., hit or miss). Hence, a prediction about an upcoming outcome error could only be made if the sensorimotor system had access to information about the cause of the error, either from internal information (about movement execution) or from external information (about the manipulation). Since information about an external manipulation was absent in case of

the self-induced errors, the observed error-related negativity can be interpreted as a predictive process that designates observed errors as self-generated tagging them as relevant for subsequent behavioral adjustments. These adjustments in trials following self-generated performance errors manifested as larger corrections in release velocity and release angle after internal errors had been detected compared to external errors and compared to trials in which the target was hit.

Our results are in line with previous studies suggesting a role for internally generated predictions about the sensory consequences of (to-be) executed movements for the self-other distinction and thus the experience of agency of observed environmental events. Here, we show that a similar mechanism could also be used to distinguish between self-generated and "other-generated" errors. Accordingly, behaviorally relevant errors are errors over which the visuomotor system "claims agency". Thus, our results would extend the study of Wei and Körding (2009) by adding an agency term to their model so that even very large errors, which their model would treat as irrelevant outliers, might become relevant if they are predicted by the visuomotor system and thus reflect erroneous processes within the visuomotor system (e.g., selecting the wrong action plan, misestimating the environmental conditions, or specification of inappropriate action parameters).

However, it appears that error prediction is not solely based on efferent information. The effect window of the Ne/ERN signal was set between 200 and 350 ms after ball release. Even though the onset of the grand average signal was even earlier (about 100 ms), there would still be enough time to process sensory feedback from the movement (Jeannerod, 1988). Hence, it has to be acknowledged that the prediction might be based on afferent information from movement execution, i.e., proprioceptive and visual signals concerning the arm and lever movement, in addition to information from the efference copy. Due to the complexity of the throwing task, such an integration of several sources of information might have even been necessary to yield a reliable prediction at all. Several studies have shown that humans integrate information from different sources to achieve a more reliable prediction of action effects (Desmurget & Grafton, 2000; Shadmehr et al., 2010; Wolpert et al., 1995). Conversely, previous research also indicates that reduced sensory information about movement execution in a complex throwing task hinders the prediction of the terminal action outcome (Joch et al., 2018). Furthermore, other studies, which used comparable complex motor tasks, also found a delayed onset of the Ne/ERN (Anguera, Seidler, & Gehring, 2009; Joch et al., 2017, 2018; Maurer et al.,

2015; Torrecillos, Albouy, Brochier, & Malfait, 2014), indicating that the onset of the Ne/ERN and the complexity of the task might be deeply intertwined. Yet, despite the possible influences of sensory information from movement execution, neither information about the action effect nor about the action outcome contributed to the Ne/ERN signal, which supports its association with outcome error prediction.

In addition to the relatively late onset of the Ne/ERN signal, its amplitude was found to be diminished compared to other studies. This might be related to performance improvement and learning in this complex motor task. It is important to note that the task specific forward model is not innate to the system, but has to be learned along with the task. Thus, reliability or/and accuracy of the prediction increases with learning (Jordan & Rumelhart, 1992). Participants of the present study had learned the task to a point where we could have expected them to have generated an adequate forward model enabling them to predict the terminal action outcome of their throwing movements (Joch et al., 2017, 2018; Maurer et al., 2015). However, the hit rate continued to improve beyond the two practice sessions. Hence, it cannot be ruled out that learning was still proceeding. This might have had an influence on the quality of the forward model and hence the accuracy of the prediction. As a result, the Ne/ERN might have been attenuated. Nevertheless, this should not have affected the comparison between hits, self-induced, and externally manipulated errors as we chose the trials evenly from all three experimental sessions.

Ne/ERN and FRN behave complementary with respect to internal and external errors

With respect to *postdictive* processes, we found clear differences in the EEG between hits, self-induced errors, and externally manipulated errors 200–300 ms after the outcome feedback had become available. We found an FRN in both types of error trials, but a higher amplitude of the FRN in externally manipulated errors. Both error types had been presented with the same external outcome feedback on the computer screen. However, the manipulation was not noticeable by the participants. It was unsystematic, and since the manipulated errors were hits from the sensorimotor system's perspective, they could not be predicted. Hence, the difference in the FRN effect window can only be explained by a complementary relationship between Ne/ERN and FRN. In case of self-induced errors, the Ne/ERN is the first indication that the action outcome is worse than expected. Assuming a 100% accurate prediction, terminal outcome feedback

does not provide new information. Hence, the FRN representing error *postdiction* on the basis of outcome feedback can be regarded obsolete with respect to error detection. This would entail the presence of a Ne/ERN and the absence of a FRN in self-induced errors on the one hand, and the absence of a Ne/ERN and the presence of a FRN in externally manipulated errors on the other hand. However, prediction can never be expected to reach 100% reliability due to inherent noise in efferent and afferent streams within the system. In addition and related to this, error feedback/*postdiction* is necessary to compare with error *prediction* in order to account for noise, improve future predictions, and to attribute the error to a cause (Wolpert & Flanagan, 2001). Hence, it is plausible that the FRN is still manifest even with a preceding Ne/ERN, but it should be smaller. Our data are in line with this. The FRN in externally manipulated errors was larger and the Ne/ERN was smaller as compared to self-induced errors and vice versa. Regarding the reinforcement learning theory, we can interpret the larger Ne/ERN in self-induced errors as representing the first indication that the outcome of an action (in our case a throw) was worse than expected (Holroyd & Coles, 2002); and that this indication was based on prediction. The larger FRN in external errors (i.e., throws that would have hit the target but had been manipulated to miss it) confirms that the error was not predicted in these trials, but valuation of the terminal action outcome was based on outcome feedback.

In general, the complementarity between Ne/ERN and FRN in internal and external errors is in agreement with the studies mentioned in the introduction by Gentsch et al. (2009), Steinhauser and Kiesel (2011), and Padrao et al. (2016), who found the Ne/ERN to correlate with self-generated internal errors, while externally-generated errors were followed by a FRN. In these studies, this effect was much stronger as compared to the present study. This can be explained in terms of the difference regarding the level of the visuomotor hierarchy on which errors were committed. In stimulus-response tasks, errors are typically committed on the decision level and demand a binary choice. Hence, a prediction of an error is relatively easy. In contrast, errors on the motor level can arise from a redundant (i.e., infinite) combination of movement variables. For instance, the prediction of motor errors in the presently used goal-oriented throwing task requires a good knowledge of the mapping between release angle, release velocity, and movement outcome that has to be learned, but will never reach perfection. Thus, prediction and attribution errors occur more often in such tasks and have a stronger effect on the averaged ERP signals.

Behavioral adaptations are larger after internal errors

With respect to behavioral adjustments, we observed, as expected and already mentioned, larger corrections in the trials after self-induced error trials as compared to externally manipulated errors. However, we also found kinematic corrections after external errors and after successful trial (hits). Corrections in velocity were similar after external errors and hits, while corrections in release angle were higher for external errors than for the hits. These effects can be explained threefold: First, minimal corrections occur constantly during learning processes, even in successful trials as these are not perfect hits all the time (the target can be centrally hit or only touched). Second, unsystematic variability (noise) affects movement execution and, hence, has an influence on changes from one trial to another. Third, manipulated errors might not always be attributed correctly as coming from an external source and, in consequence, are answered by corrective behavior. Yet, in general, we can conclude that behavioral adjustments are more strongly related to internally attributed and thus relevant errors.

Conclusion and outlook

In conclusion, our results support the assumption that the Ne/ERN, as a neural correlate of error prediction, tags internal, self-generated errors as relevant for behavioral adaptations, not only in stimulus-response tasks, but also in more naturalistic, complex motor tasks like throwing. In contrast, the amplitude of the FRN seems to depend on whether or not the motor system has already predicted an error in the ongoing trial. Hence, external error attribution is marked by a larger FRN amplitude. What still remains to be examined is whether the complementarity between Ne/ERN and FRN is differentially expressed in the course of learning. Theoretical considerations (Holroyd & Coles, 2002) and experimental data of an auditory-motor mapping task (Lutz et al., 2013) suggest that the Ne/ERN signaling error prediction should increase with learning since error processing must rely on the *postdictive* function of the FRN at first. Whether this also affects error attribution and whether the FRN, in contrast, attenuates as predictive processes gain importance for error detection has to be finally revealed.

Keywords: error prediction, error attribution, motor error, error-related negativity, feedback-related negativity

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