

Electrophysiological Evidence for Action-Effect Prediction

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A central function of the human brain is prediction. Influential theoretical views suggest that we form predictions about forthcoming sensory outcomes that follow from our own actions and that anticipation of these outcomes is fundamental for action control. However, little is known about how predicted outcomes are represented at the neural level. We hypothesized that neural activity reflecting the anticipation of outcomes should precede action initiation. Following computational theories on action control, anticipation should be reflected in an outcome-selective reduction in neural activity. To test this, the present study recorded scalp electroencephalography to show that brain activity reflects action-effect specific representations before response initiation. We harnessed frequency entrainment to tag neural activity specific for particular action-effects. Participants engendered visual action-effects that were presented in flickering frequencies of 6 or 10 Hz, either according to a fixed cue-response mapping (Experiment 1) or freely chosen (Experiment 2). Results showed that perception of action-effects entrained a steady-state visual brain response specific to the perceived action-effect at either 6 or 10 Hz. More important, neural pattern reflecting action-effect specific representations emerged even before a response was given (i.e., without any visual stimulation). In line with theoretical accounts, perception of action-effects led to a specific increase in neural activity, while prediction of action-effects led to a specific decrease in neural activity. These findings provide neural evidence for the anticipation of action-effects before response initiation, supporting major theories of action control.

Keywords: ideomotor theory, prediction, voluntary action, electroencephalography (EEG)

Humans are not reactive but anticipatory creatures. We constantly form expectations about future events and use them to guide our decisions and actions (von Helmholtz, 1866/1925). Therefore, it has been suggested that the brain generates predictions about forthcoming sensory information in order to match this anticipated input against the observed input (Friston, 2005; see also Wolpert & Ghahramani, 2000). In other words, predictions serve as a template against which actual evidence is compared

(Summerfield & Egner, 2009; for a review, see de Lange, Heibron, & Kok, 2018).

However, predictions are not only relevant for the interpretation of sensory information but are also fundamental for action control. For instance, William James argued that any voluntary action starts with the anticipation of its sensory consequences or action-effects (James, 1890). These action-effects can refer to perceptual changes of one's own body while moving (e.g., experiencing the proprioceptive feedback and the visual change of a finger pressing the piano keys) as well as to perceptual changes in the environment caused by the movement (hearing the tone produced by the piano key). Not surprisingly, James considered action-effects in the environment to be most important (cf. James, 1890), because in everyday behavior, a certain change in the environment can be achieved with an innumerable number of body movements. Now, ideomotor theory suggests that action-effects precede movements, because action-effects have a generative function (Hommel, 2013; for a review, see Badets, Koch, & Philipp, 2016; Shin, Proctor, & Capaldi, 2010). Specifically, anticipating an action-effect automatically activates those motor patterns that caused the corresponding effect in the first place. This notion received support from numerous behavioral studies showing that action-effects modulate the planning and execution of responses (e.g., Elsner & Hommel, 2001; Hommel, 1996; Kunde, 2001; Kunde, Koch, & Hoffmann, 2004). Regarding the cognitive implementation of action-effects, influential models of action control have proposed that predicted action-effects are used to suppress perceptual processing of these expected outcomes (Bays & Wolpert, 2007; Wolpert, Ghahramani, & Jordan, 1995). Indeed, there is support from neuroimaging work

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David Dignath, Andrea Kiesel, and Bernhard Pastötter developed the study concept, design the study, and performed the data collection. Bernhard Pastötter and David Dignath performed the data analysis, and all authors discussed the results. David Dignath and Bernhard Pastötter drafted a first version of the manuscript, and Andrea Kiesel and Christian Frings provided critical revisions. All authors approved the final version of the manuscript for submission.

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for this view, showing that the perception of predictable sensory consequences of actions is associated with reduced activity in sensory brain areas (e.g., Blakemore, Wolpert, & Frith, 1998; Leube et al., 2003). However, little is known about how such sensory predictions of the to-be produced outcomes are represented at the neural level regarding the preparation of actions and the anticipation of action effects.

Preparation of actions often has been associated with the readiness potential, which can be measured with electroencephalography (EEG), as an indicator of motor preparation and the intention to act (Kornhuber & Deecke, 1965; Libet, 1985). Interestingly, the amplitude of the readiness potential is increased for actions that are consistently followed by action-effects (Reznik, Simon, & Mukamel, 2018; Vercillo, O'Neil, & Jiang, 2018). This can be taken as evidence for an unspecific expectation, that is, a general preparedness to act. Furthermore, studies that recorded hemodynamic brain activity before response execution reported increased activity in sensory-motor areas, specific for the perception of the response effector used (e.g., the hand or the face). This suggests that body-related aspects of action-effects are coded in the brain before movement initiation (Kühn, Keizer, Rombouts, & Hommel, 2011; van Steenbergen et al., 2017).

In the present research, we used EEG to show that leading brain activity reflects predictions of newly learned action-effects in the environment. The results of two experiments are reported. Experiment 1 used a forced-choice task, whereas Experiment 2 used a free-choice task, in which participants were free to decide on each trial which of two response keys to press. Critically, this procedure eliminates any confounds in terms of learned associations between cues and action-effect learning. In contrast to previous functional MRI (fMRI) research that used a similar task (Kühn, Seurinck, Fias, & Waszak, 2010), the high temporal resolution of EEG allows us to de-confound neural activity related to action-effect anticipation, response execution, and the perception of action effects. Going beyond previous fMRI research that used natural, body-specific action-effects that were highly overlearned (e.g., moving one's own hand changes the perception of the hand), we used newly learned action-effects that resulted from an arbitrary mapping between two very similar responses with two visual action-effects in the environment (e.g., pressing a left key resulted in the presentation of the image of a cat). And finally, extending previous research on the readiness potential, we harnessed frequency entrainment to tag the neural signature of particular action-effect representations (Keil, Müller, Ray, Gruber, & Elbert, 1999). This suggests that neural markers of predictions preceding an action should be specific to the to-be produced action-effects.

Participants produced visual action-effects presented in different flickering frequencies (6 or 10 Hz) that were expected to modulate a steady-state visual evoked potential in EEG power (SSVEP power) at 6 or 10 Hz, respectively, during perception of action-effects. Indeed, it has been shown that observation of a specific flicker frequency leads to increased activity in the EEG for this frequency (e.g., Herrmann, 2001). Therefore, we predicted an action-effect specific increase in SSVEPs during perception of action-effects (e.g., perception of a 6-Hz flicker should lead to increased EEG activity for 6 Hz relative to 10 Hz).

More important, regarding the anticipation of action-effects, we hypothesized that frequency-tagged representations of action-effects would (re)emerge in the EEG in the absence of any visual

stimulation prior to responding. Indeed, frequency tagging has also been used in previous work to tag episodic memory retrieval (Lewis, Schriefers, Bastiaansen, & Schoffelen, 2018; Wimber, Maaß, Staudigl, Richardson-Klavehn, & Hanslmayr, 2012; but see Price & Johnson, 2018). More precisely, we predicted a modulation of preresponse EEG power at 6 or 10 Hz that should be specific to the intended action-effect. In addition, following the view that action-specific predictions are used to suppress perceptual processing of expected outcomes (Bays & Wolpert, 2007; Wolpert et al., 1995) and the finding that preparation of voluntary actions is often accompanied by a general decrease in oscillatory activity (Pogosyan, Gaynor, Eusebio, & Brown, 2009; Schoffelen, Oostenveld, & Fries, 2008; see also Keitel, Keitel, Benwell, Daube, Thut, & Gross, 2019), we predicted a decrease in preresponse power changes during anticipation of action-effects that should be frequency specific for the respective action-effect (e.g., anticipation of a 6-Hz flicker should lead to decreased EEG activity for 6 Hz relative to 10 Hz). Statistically, this should become apparent in a disordinal interaction of EEG frequency and (anticipated) flicker frequency.

Method

Experiment 1 was a pilot study and used a forced-choice task. Experiment 2 was identical to Experiment 1, except that a free-choice procedure was used in which the imperative cue no longer predicted a specific response to assess action-effect anticipation for voluntary actions. Thus, Experiment 2 allows tracking action-effect anticipation for voluntary actions. In both experiments, we measured scalp EEG and examined SSVEP power changes related to perception during action-effect presentation and preresponse EEG power modulations related to action-effect anticipation.

Participants

Thirty-two (25 female, mean age = 21.47; $SD = 2.83$) healthy volunteers participated in Experiment 1. Based on the results of Experiment 1, we ran power analyses using G*Power (Faul, Erdfelder, Buchner, & Lang, 2009), which suggested a sample size of $N = 28$ to detect a medium effect of $f = 0.25$ (with $\alpha = .05$, two-sided, $1 - \beta = .80$, and correlation among repeated measures = .6). Twenty-eight (18 female, mean age = 23.57; $SD = 4.79$) participants were included in Experiment 2 (data of 4 participants could not be analyzed due to technical problems during recording or heavy artifacts in the EEG; data of these participants were replaced by 4 new participants, leaving $N = 28$ for the analysis). All participants gave written informed consent for participation in the experiment, which received ethical approval by the Ethics Committee of the University Freiburg (ref. 81/17).

Stimuli and Procedure

We adapted a standard action-effect paradigm (Elsner & Hommel, 2001) by instructing participants to produce one of two distinct visual action-effects while recording EEG. We did not include a separate learning phase, since previous research has shown that action-effects can be acquired even after a few trials (Wolfensteller & Ruge, 2011). On each trial, participants fixated a central asterisk for 1,500 ms, which changed its color to red or

green (presented for 1,000 ms). Participants responded to the color change with a left or right key press (“d” or “l” key on a QWERTZ keyboard). In Experiment 1, participants completed 120 single trials with a forced-choice procedure using a fixed cue-response mapping (e.g., green > left; counterbalanced across participants).¹ Participants received feedback for late (>1,000 ms) or incorrect responses (2,000 ms; only Experiment 1). Correct responses triggered the presentation of a visual action effect after a delay of 50 or 1,500 ms, that is, the *action-effect delay* (key-delay mapping was counterbalanced across participants in Experiment 1 and within participants in Experiment 2 with a reversal of action-effect delay mapping after half of the experimental trials). The visual action-effect depicted a line drawing of a sheep or a cat presented for 2,000 ms, flickering either in 6 or 10 Hz (no action effect was presented following late or incorrect responses). The mapping of visual stimulus (cat vs. dog) and flicker frequency (6 Hz vs. 10 Hz) was counterbalanced across participants and an acoustic action-effect (sound of a sheep or cat for 700 ms at about 55 dB). In Experiment 2, participants completed 720 single trials with a free-choice procedure preceded by 16 training trials. Here, participants were instructed to choose freely one of the two response keys upon the onset of the green asterisk. They were explicitly instructed to decide spontaneously and not to use any kind of strategy. Preplanning of responses was discouraged by presenting a no-go cue (a red asterisk) in 25% (i.e., 135) of the 720 trials.

Design

Both experiments used a within-subject design with the factors EEG frequency (i.e., the frequency band analyzed, 6 Hz vs. 10 Hz) and flicker frequency (i.e., the frequency of the action-effect stimulus, 6 Hz vs. 10 Hz). Mean power changes in the EEG served as the dependent variable. We conducted two analyses that focused either on EEG power changes during action-effect perception (i.e., SSVEP power) or on EEG power changes during action-effect anticipation (i.e., preresponse power). We also included the action-effect delay (50 vs. 1,500 ms) as an additional factor to test whether changes in temporal contiguity would affect EEG marker of action-effects (see Dignath, Pfister, Eder, Kiesel, & Kunde, 2014; Elsner & Hommel, 2004). This did not affect the EEG results reported here, which is important for the present analysis; see Results for details.

EEG Recording

In Experiment 1, scalp EEG was recorded from 61 equidistant active electrodes (ActiCAP; Brain Products, Gilching, Germany). Electrode-skin impedance was kept below 20 k Ω . Electrode Cz served as common reference. Signals were digitized with a sampling rate of 500 Hz and amplified between 0.15 and 250 Hz with a notch filter at 50 Hz, removing power-line noise, which has a 50-Hz frequency in Europe (BrainAmpMR plus, BrainVision Recorder; Brain Products). In Experiment 2, scalp EEG was recorded from 32 active electrodes positioned according to the 10–10 electrode system with reference to electrode Cz (ActiChamp; Brain Products). Electrode-skin impedance was kept below 20 k Ω . Signals were digitized with a sampling rate of 500 Hz and amplified between 0.15 and 140 Hz. Additional face electrodes were used to monitor eyeblinks and the vertical and horizontal electrooculogram (EOG).

EEG Analyses

EEG recordings were rereferenced offline against average reference and EOG corrected using calibration data to generate individual artifact coefficients (Ille, Berg, & Scherg, 2002), as implemented in BESA Research (v7.0 June 2018; BESA Software, Gräfelfing, Germany). Remaining artifacts were marked by careful visual inspection. EEG data were segmented into epochs ranging from -2 to 5 s around the onsets of stimuli, responses, and effects. To avoid filter artifacts at the edges of the segments, further analyses were restricted to intervals ranging from -0.5 to 3.5 s around the onsets of stimuli, responses, and effects, respectively. Segments containing artifacts and segments with response errors (in Experiment 1) were discarded from further analyses.

To transform EEG data into the time-frequency domain, a complex demodulation algorithm as implemented in BESA was used. The algorithm consists of a multiplication of the time-domain signal with a complex periodic exponential function, having a frequency equal to the frequency under analysis, and subsequent low-pass filtering. The low-pass filter is a finite impulse response filter of Gaussian shape in the time domain, which is related to the envelope of the moving window in wavelet analysis. The data were filtered in a frequency range from 2 to 30 Hz. Time resolution was set to 78.8 ms (full-power width at half maximum, FWHM) and frequency resolution was set to 1.42 Hz (FWHM). Time-frequency data were exported in bins of 50 ms and 1 Hz.

In time-frequency analysis, both SSVEP power modulations induced by perceiving action-effects and preresponse EEG power modulations induced by action-effect anticipation were calculated in relation to power in a 0.2-s baseline interval, which was set from -0.35 to -0.15 s before color change of the asterisk. Power changes were determined by calculating the temporal-spectral evolution, that is, power changes for all time–frequency points with power increases or decreases at time point t and frequency f in relation to mean power at frequency f over the preceding baseline interval for each electrode and condition (Pfurtscheller & Arani-bar, 1977).

In SSVEP power analysis, inferential statistics focused on mean power changes during the 2-s action-effect presentation over electrodes O1, Oz, and O2 at 6 and 10 Hz. Occipital electrodes were used because SSVEP power effects are largest over occipital sites (e.g., Gulbinaite, van Viegen, Wieling, Cohen, & VanRullen, 2017). In preresponse EEG power analysis, we focused on mean power changes averaged from -0.35 to -0.15 s before key press. To identify relevant electrodes, we examined whether there were significant interactions between EEG frequency and flicker frequency for each single electrode. To account for multiple testing, a two-stage randomization procedure was carried out. At first, for each electrode, a t test (two-sided) on the difference between difference scores was calculated in order to investigate which electrodes showed a significant Flicker Frequency \times EEG Frequency interaction ($p < .05$). Thereafter, a randomization test using 100,000 permutations was run, in which we shuffled the order of difference scores consistently across electrodes (see Blair & Karniski, 1993; Pastötter, Schicker, Niedernhuber, & Bäuml,

¹ Experiment 1 was planned as a pilot experiment, administered within a larger study and therefore had fewer trials.

2011). This procedure evaluates whether a given number of electrodes exhibiting a significant interaction is expected by chance. If the p value (p_{corr}) of this randomization test was below .05, then less than 5% of the permutation runs exhibited equal or more electrode sites with a significant Flicker Frequency \times EEG Frequency interaction.

Following ideomotor theory, we hypothesized that participants learn the action-effect associations and therefore anticipate the flickering of the intended action-effect before response initiation. Thus, prereponse EEG power changes (in percent), averaged from -0.35 to -0.15 s before key press, were analyzed as a function of EEG frequency (6 Hz, 10 Hz) and (anticipated) flicker frequency.

Results

Only correct trials were used for reaction time (RT) and EEG analysis in Experiment 1. To avoid influences of outliers on RT data, the median RTs were computed for each participant.

Behavioral Results

In Experiment 1, the median RT was 439 ms ($SD = 48$ ms); participants showed on average $M = 2.89\%$ ($SD = 3.38\%$) incorrect response errors and $M = 2.58\%$ ($SD = 2.82\%$) late response errors. In Experiment 2, the mean median RT was 398 ms ($SD = 51$ ms); participants showed $M = 1.36\%$ late response errors ($SD = 1.28\%$) and $M = 3.77\%$ ($SD = 3.24\%$) no-go errors. Relative frequencies of left and right key presses were computed for each participant; a response proportion of 44.5–55.5% or more extreme was classified as a significant deviation from an equal response distribution (corresponding to a two-category chi-square goodness-of-fit test with a significance level at $\alpha = .15$; see Dignath et al., 2014). No participants had to be excluded according to this criterion. In line with previous studies, we observed a significant influence of the delay between actions and effect presentation on the median RT. This delay-anticipation effect (prolonged responses for long relative to short delays) was significant in Experiment 1 ($\Delta = 9$ ms; $t_{31} = 2.55$, $p = .016$, $d = .045$) and Experiment 2 ($\Delta = 5$ ms; $t_{27} = 2.12$, $p = .044$, $d = .039$).

EEG Results

Perception. In both experiments, significant SSVEP power changes over occipital electrodes emerged (see Figure 1). In Experiment 1, the Repeated-measures Analysis of Variance (RM-ANOVA) with the factors of EEG frequency (6 Hz vs. 10 Hz) and flicker frequency (6 Hz vs. 10 Hz) showed a significant main effect of EEG frequency, $F(1, 31) = 8.084$, $p = .008$, $\eta_p^2 = .207$, due to generally larger 6-Hz than 10-Hz power changes, but no main effect of flicker frequency, $F(1, 31) < 1$. More important, the RM-ANOVA showed a significant interaction between the two factors, $F(1, 31) = 12.263$, $p = .001$, $\eta_p^2 = .283$, indicating frequency specificity of SSVEP effects. Indeed, 6-Hz power changes were larger for 6-Hz than for 10-Hz flickers, $t_{31} = 2.729$, $p = .010$, $d = .482$, whereas 10-Hz power changes were larger for 10-Hz than for 6-Hz flickers, $t_{31} = 2.400$, $p = .023$, $d = .424$. Consistently, in Experiment 2, the RM-ANOVA showed a significant main effect of EEG frequency, $F(1, 27) = 32.545$, $p < .001$,

$\eta_p^2 = .547$, due to generally larger 6-Hz than 10-Hz power changes, but no main effect of flicker frequency, $F(1, 27) < 1$. Again, both factors interacted significantly, $F(1, 27) = 5.644$, $p = .025$, $\eta_p^2 = .173$. Indeed, 6-Hz power changes were larger for 6-Hz than for 10-Hz flickers, $t_{27} = 2.084$, $p = .047$, $d = .394$, whereas the difference for 10-Hz power was not significant, $t_{27} = 1.403$, $p = .172$, $d = .265$.

Anticipation. Critically, in both experiments, significant pre-response EEG power modulations related to action-effect anticipation emerged (see Figure 1). Randomization tests, which evaluated whether a given number of electrodes showing a significant interaction effect were expected by chance (see Method section), revealed a reliable and disordinal interaction between the factors of EEG frequency (6 Hz vs. 10 Hz) and (anticipated) flicker frequency (6 Hz vs. 10 Hz) over 10 (out of 61) electrodes in Experiment 1, $p_{\text{corr}} = .042$, and over 7 (out of 32) electrodes in Experiment 2, $p_{\text{corr}} = .020$, mainly over parietal sites.² In Experiment 1, pairwise comparisons showed that 6-Hz power changes were smaller for (anticipated) 6-Hz than for (anticipated) 10-Hz flickers, $t_{31} = 2.848$, $p = .008$, $d = .503$, whereas 10-Hz power changes were smaller for (anticipated) 10-Hz than for (anticipated) 6-Hz flickers, $t_{31} = 2.895$, $p = .007$, $d = .512$. Action-effect delay (50 ms vs. 1,500 ms) did not affect these results ($p = .413$). In Experiment 2, 6-Hz power changes were also smaller for (anticipated) 6-Hz than for (anticipated) 10-Hz flickers, $t_{27} = 3.274$, $p = .003$, $d = .619$, whereas 10-Hz power difference was not significant, $t_{27} = 1.073$, $p = .293$, $d = .203$, albeit the difference was at a descriptive level in the expected direction.³ Again, action-effect delay did not affect the results ($p = .198$).

Discussion

In the present research, we aimed to show neural evidence for action-specific predictions. Results established that electric brain activity in the EEG precedes response initiation. More specifically, this neural response reflected a selective signature of anticipated action-effects without any visual stimulation present: Flickering frequencies of intended action-effects entrained a specific steady-state brain response at either 6 or 10 Hz, which preceded initiation of the respective response.

This finding provides evidence for neural predictions that are specific to the outcomes of an action. This is in line with major theoretical views on sensory prediction and action control (Friston & Kiebel, 2009; Hommel, 2013) and extends earlier studies that used fMRI to show that effector-specific activation precedes responding (Kühn et al., 2010, 2011; Ruge, Müller, & Braver, 2010;

² In Experiment 2, the finding was also significant when trials that followed no-go events were excluded in the analysis; again, the results revealed a reliable and disordinal interaction over 7 (out of 32) electrodes, $p_{\text{corr}} = 0.019$.

³ In Experiment 2, the pairwise comparison revealed that the effect for the anticipation of a 10-Hz frequency was not significant. Given that also the perceptual effect in the 10-Hz frequency was not significant, it might be less surprising that the anticipation effect was not significant, too. Thus, based on this data pattern, we do not think that there might be a specific disadvantage of anticipation effects in 10-Hz compared to 6-Hz frequencies, but rather assume that for this specific experiment, the representation of the 10-Hz frequency was not sufficiently strong. Please note, however, that both the anticipation and perception effects for the 10-Hz frequency were significant in Experiment 1.

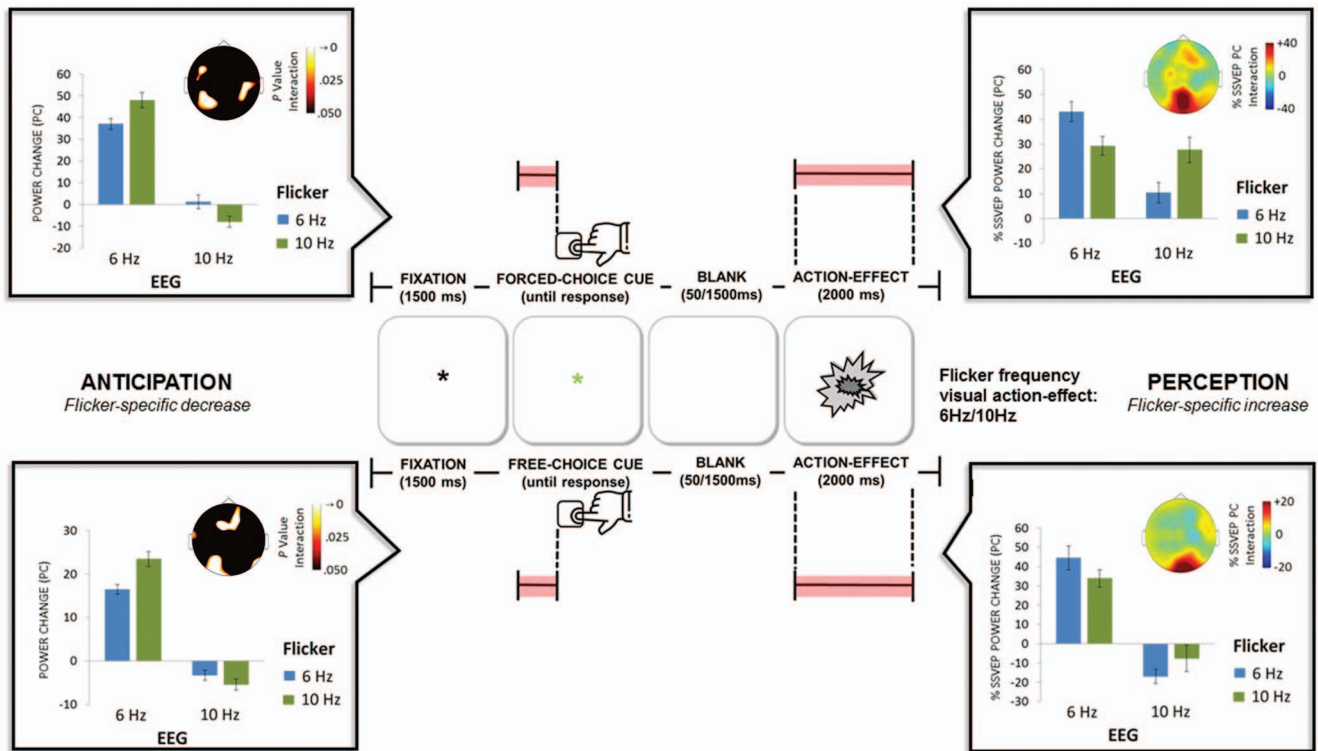


Figure 1. Trial sequence and EEG results of Experiment 1 (upper panel) and Experiment 2 (lower panel). Participants responded to two differently colored cues according to a specific cue-response rule (Experiment 1) or to a single go-cue with a freely chosen response (Experiment 2). Each response triggered a visual action-effect that flickered either in 6 Hz or 10 Hz for 2 s. Action-effects followed responses with a fixed delay of either 0.05 s or 1.5 s. The left side of the figure shows anticipatory mean power changes (PC, in percent) as a function of electroencephalography (EEG) frequency (6 Hz, 10 Hz) and flicker frequency of the intended action-effect (6 Hz, 10 Hz) in a time window of -0.35 to -0.15 s before response. The right side shows perceptual mean steady-state visual evoked potential in EEG (SSVEP) PC as a function of EEG frequency (6 Hz, 10 Hz) and flicker frequency (6 Hz, 10 Hz) during the 2 s of stimulus presentation. Color coding of topographical maps shows the SSVEP PC interaction, that is, the difference in 6-Hz power between 6-Hz and 10-Hz flickers minus the difference in 10-Hz power between 6-Hz and 10-Hz flickers. Error bars indicate within-subject standard errors (Cousineau, 2005). See the online article for the color version of this figure.

van Steenbergen et al., 2017). By combining the high temporal resolution of EEG and the specificity of action-effect frequency tagging with a free-choice task, Experiment 2 provides direct support for effect-based accounts of action control like ideomotor theory.

Interestingly, previous research that investigated predictive neural activity using covariation learning (e.g., a specific stimulus predicts the occurrence of another stimulus) suggested that expectancies are reflected by increased neural activity (e.g., de Lange, Rahnev, Donner, & Lau, 2013; Donner, Siegel, Fries, & Engel, 2009; Kok, Mostert, & de Lange, 2017). In contrast, the present research observed a reduction in neural activity during anticipation of the action-effect stimuli. Although this might seem surprising, this pattern is actually predicted by computational models, which assume that a “forward model” in the motor system suppresses activity in expected sensory units (Bays & Wolpert, 2007; Wolpert & Ghahramani, 2000), and animal models, which show that action-specific predictions lead to inhibition of expected sensory consequences (cf. de Lange et al., 2018; see also Blakemore et al., 1998;

Miall, Weir, Wolpert, & Stein, 1993, for neurophysiological evidence linking this mechanism to the cerebellum; for a review, see Bastian, 2006). In addition, the pattern is in line with earlier findings showing that preparation of voluntary actions is often accompanied by a general decrease in oscillatory brain activity (e.g., Keitel et al., 2019; Pogossyan et al., 2009). This suggests the possibility that predictive neural activity is very different for goal-directed actions compared to perceptual detection tasks, although more direct tests are needed to investigate and understand these differences in more detail.

Alternatively to the suppression (or cancelation) account, it has been suggested that action sharpens sensory representations of expected outcomes (Kok, Jehee, & de Lange, 2012). According to this view, reduced neuronal activity is accompanied by an improved, sharpened representation of sensory consequences. Such an interpretation dovetails with a recent observation of Khalighinejad and colleagues showing that voluntary actions relative to stimulus-driven actions were preceded by a reduction in variability of the readiness potential (RP), which was accompanied by a

reduction in premotor beta power (Khalighinejad, Schurger, De-santis, Zmigrod, & Haggard, 2018; see also Yon, Gilbert, de Lange, & Press, 2018). This reasoning would also be in line with recent theoretical models that explain the sensory attenuation effect in terms of a preactivation of anticipated action effects (Waszak, Cardoso-Leite, & Hughes, 2012) and the information-via-desynchronization view on oscillatory brain function, according to which neural desynchronization (i.e., decrease in oscillatory power) is positively related to the richness of information represented in the human brain (Hanslmayr, Staudigl, & Fellner, 2012). While the present study was not designed to arbitrate between suppression and sharpening accounts of perception and action control, it provides new methods to test theoretical models of sensory action-effect attenuation in future work.

In addition, the present results also might be informative for research on voluntary actions. In theory, it has been suggested that forced-choice tasks (as used in previous fMRI research) delegate control to an exogenous stimulus (i.e., the cue) and thus contradict the very notion of an endogenous, voluntary action (Brass & Haggard, 2008; Passingham, Bengtsson, & Lau, 2010). Consequently, studies interested in voluntary actions should use free-choice tasks in which participants can decide between different response alternatives on each trial (e.g., Jahanshahi et al., 1995; Pesaran, Nelson, & Andersen, 2008; see Passingham et al., 2010, for a review). Indeed, research suggested that action-effect anticipation differs between voluntary and stimulus-driven actions, and it is currently debated whether this is due to learning of action-effect associations or expression of effect-based action control (Herwig, Prinz, & Waszak, 2007; Pfister, Kiesel, & Hoffmann, 2011). The present research provides a viable tool to assess action-effect learning independent from its expression and therefore allows testing both accounts against each other.

Action-effects specify not only what will happen but also when something will happen. Initially, it has been assumed that the time interval between an action and the corresponding effect acts as a catalyst that fosters action-effect learning for shorter relative to longer delays (Elsner & Hommel, 2004). However, more recent research suggested that we also learn to anticipate the duration of action-effect delays and that this temporal action-effect influences action initiation (Dignath, Lotze-Hermes, Farmer, & Pfister, 2018; Dignath et al., 2014; Pfister, Weller, Dignath, & Kunde, 2017; Riechelmann, Pieczykolan, Horstmann, Herwig, & Huestegge, 2017). More specifically, recollecting the temporal duration between response and effect takes time and prolongs initiation of the response; therefore, responses are slower for longer relative to shorter action-effect delays (i.e., the delay-anticipation effect). In the present research, behavioral results replicated this effect in both experiments, suggesting that participants learned to anticipate the temporal dynamics of action-effect presentation. At the same time, EEG results were not affected by the duration of action-effect delays. Taking into the account the usual caveats when interpreting null results, this could suggest two implications. First, action-effect learning might be more robust against poor temporal contiguity between actions and their effects than previously thought (cf. Elsner & Hommel, 2004). Second, the discrepant results in behavior and EEG do not support the account that participants automatically acquire integrated episodes of action-effect identity and action-effect delays (Dignath et al., 2014). Rather, they are in line with the view that temporal information is learned like any other

perceptual action-effect and retrieved independently from other action-effects (Dignath & Janczyk, 2017).

Although the present study provides the most direct evidence for anticipation of action-effects, it does not show that anticipated action-effects are causal for responding. Previous behavioral studies have used response interference tasks to show (a) that the presentation of former action-effects facilitates responses that elicit identical action-effects but interferes with responses that elicit different action-effects (Elsner & Hommel, 2001; Hommel, 1996) and (b) that anticipation of action-effects can facilitate or interfere with responses that share features of the to-be produced action-effects (Kunde, 2001; Kunde et al., 2004). Computational modeling suggested that action-effect anticipation in these behavioral tasks is indicated by an increase in the drift rate, that is, the speed at which an individual accumulates evidence for response selection (Janczyk & Lerche, 2019). In theory, this evidence accumulation can be linked to a recollection of former action-effects from memory. As a consequence, neural correlates of action-effect anticipation in EEG power (which arguably reflect such a retrieval of action-effects) could be correlated with the drift rate parameter in computational modeling of behavior.

A more direct test of a response-generative function for the reported neural marker of action-effect anticipation would require means to modulate the neural action-effect representation. Previous research has shown that transcranial alternating-current stimulation (tACS) can modulate voluntary actions in general by interfering with beta-band frequency (Pogosyan et al., 2009). Potentially, tACS could be used to selectively disrupt action-effect anticipation and to test whether this leads to impaired motor performance.

In sum, the present findings provide evidence for a neural precursor of action-specific predictions. This is in line with recent perceptual decision-making frameworks like predictive coding; at the same time, it also confirms William James's assertion that behavior is controlled via "an anticipatory image of the movement's sensible effects" (James, 1890, p. 505) by showing that electric brain activity that captures a selective signature of anticipated actions-effects precedes response initiation.

Context

The present research is a collaboration between two groups (Trier and Freiburg) that have studied action control and prediction for several years and recently proposed a new theoretical framework for action control (Frings et al., in press).

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