



Research Report

Time-based expectations entail preparatory motor activity



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ABSTRACT

Human behavior is guided by expectations that facilitate perception of upcoming events or reaction to them. In natural settings expectations are often implicitly based on time, e.g., when making a phone call one would expect to hear either a person answering (earlier) or a voicemail greeting (later). We investigated how time-based expectations can improve performance in the absence of explicit prior information on the pending stimulus or the associated response. Visual stimuli were presented after a characteristic short or long foreperiod, and a forced-choice categorization using either the left or the right hand was required. The electroencephalogram (EEG) revealed a decrease in central 9–12 Hz power over the course of the trial. Moreover, lateralized pre-motor potentials were observed which changed polarity after the short foreperiod. At stimulus onset, amplitudes of pre-motor potentials co-varied with performance, so that higher (more negative) amplitudes were associated with slower responses to unexpected targets. Altogether, the results suggest that implicit time-based expectations entail effector-specific preparatory brain activity, which is inhibited until the expected onset time of the event. Thus, time-based expectations prepare for action.

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1. Introduction

Human perception and action rely on expectations about upcoming events and possible responses to them. Valid prior information, delivered via informative pre-cues, often confer a behavioral advantage, allowing faster and more accurate responses to a cued event. Conversely, invalid prior information worsens performance compared to situations with valid or no prior information (Jackson, Miall, & Balslev, 2010; Posner & Petersen, 1990; Van Hulle, Van Damme, & Crombez, 2013;

Veldhuizen, Douglas, Aschenbrenner, Gitelman, & Small, 2011).

The neural mechanisms underlying the behavioral advantage granted by prior information are well investigated (for an overview, see Panichello, Cheung, & Bar, 2012). An illustrative example is visual spatial cueing where the location of an upcoming target in the right or in the left hemifield is indicated by an arrow in the center of the screen. Concurrent electroencephalographic recordings (EEG) typically reveal a decrease of power in the alpha frequency range (~8 to 12 Hz),

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indicative of neural excitation, at occipital electrodes contralateral to the cued location, and a corresponding increase, indicative of neural inhibition, at ipsilateral locations (Rihs, Michel, & Thut, 2009; Thut, Nietzel, Brand, & Pascual-Leone, 2006). Thus, the engagement or disengagement of spatio-topical visual cortices is contingent on the cue information, facilitating further processing of task-relevant information (Jensen & Mazaheri, 2010; Klimesch, Sauseng, & Hanslmayr, 2007). Similar anticipatory brain activity has been found for attention to object features (Snyder & Foxe, 2010; Volberg, Kliegl, Hanslmayr, & Greenlee, 2009; Volberg, Wutz, & Greenlee, 2013), or to visual object categories like faces or places (Esterman & Yantis, 2010). Prior information can also facilitate action, so that events requiring left or right limb movements increase activity in the respective contralateral compared to ipsilateral motor cortex (Witt, Laird, & Meyerand, 2008). All in all, the available results show that prior information about upcoming events increases activity in relevant cortices and facilitates processing of expected events.

Expectations are often implicitly coupled with time. Hearing a knock at the door of one's office, one would expect someone to enter within the next few seconds – but if no one enters by that time, one would expect another knock at the door. Such time-based expectations are highly prevalent in everyday life, in human communication as well as in human–machine interactions (Finlayson & Corley, 2012; Heller, Arnold, Klein, & Tanenhaus, 2015; MacGregor, Corley, & Donaldson, 2010; Thomaschke & Haering, 2014). Importantly, time-based expectations are not simply expectations about time durations. It is known that when the same event can occur after different foreperiods, reactions are faster if the foreperiod duration is highly predictable (Steinborn, Rolke, Bratzke, & Ulrich, 2008, 2009, 2010). Multiple processes profit from such temporal predictability, including response selection (Los, 2013) and visuo-spatial perception (Cravo, Rohenkohl, Wyart, & Nobre, 2013; Rolke, Festl, & Seibold, 2016; Seibold, Bausenhardt, Rolke, & Ulrich, 2011; Seibold & Rolke, 2014). Unlike expectations of time durations, time-based expectations refer to expectation of events: The elapsed time relative to an initial event (the knock at the door) serves as a cue for a subsequent event (someone entering the office). Accordingly, time-based expectations generalize to broader time intervals, whereas expectations of time durations are rather specific to the absolute duration of the foreperiods (Thomaschke, Kunchila, & Dreisbach, 2015; Thomaschke, Wagener, Kiesel, & Hoffmann, 2011).

To date, time-based expectations have been investigated in only a handful of studies. Typically, different visual targets are presented after either a short or a long foreperiod. Observers learn contingencies between time durations and events and, with practice, respond faster and more accurately to events that were expected based on the elapsed time (Thomaschke & Dreisbach, 2015; Thomaschke et al., 2011; Wagener & Hoffmann, 2010). Thus, time-based expectations have the same behavioral effect as expectations induced by explicit pre-cues (Posner & Petersen, 1990).

Intriguingly, however, it is still unclear which particular stimulus or task information observers utilize to improve their performance in time-based expectations. Observers are mostly unaware of the temporal structure or time and event

contingencies in the task, making the cue utilization subconscious and unintentional (Coull & Nobre, 2008). Unlike in conventional cueing paradigms, a temporal cue does not direct the observer's attention to a specific quality of the target event, for example the spatial location (e.g., Rihs et al., 2009), the stimulus category (e.g., Esterman & Yantis, 2010) or the associated response (e.g., Smulders & Miller, 2012, pp. 209–229). It therefore remains unknown which perceptual, cognitive or motor processes underlie time-based expectations (cf. Thomaschke & Dreisbach, 2013; Thomaschke, Hoffmann, Haering, & Kiesel, 2016). The present EEG study specifically set out to investigate one of those candidate mechanisms: The role of preparatory motor activity in time-based expectations. Given that expectations induce brain activity in task-relevant cortices (Jensen & Mazaheri, 2010; Klimesch et al., 2007), neural activity during short or long foreperiods should vary within corresponding motor areas if preparation for action is a factor.

The participants performed a visual categorization task where two possible targets, a triangle or a circle, were preceded by a characteristic short or long foreperiod. A performance advantage was expected for trials in which the target matched the expectation, i.e., for trials with frequent compared to infrequent combinations of foreperiod and target category. Once this performance advantage was confirmed, we tested the hypothesis that this effect is due to motor preparation. Two targets were mapped onto different left or right response hands and the lateralized readiness EEG potential was recorded (LRP, Eimer, 1998; Smulders & Miller, 2012, pp. 209–229). The LRP is a traditional measure of preparatory motor activity, calculated by subtracting the event-related potential (ERP) measured at ipsilateral central electrodes from the ERP measured at contralateral central electrodes. Negative values indicate stronger neural activity in the relevant motor areas and thus a proper response preparation (Faugeras & Naccache, 2016; Sangals, Sommer, & Leuthold, 2002). If time-based expectations rely on preparatory motor activation, then corresponding LRPs should occur, favoring different responses after short and long foreperiods.

Alternatively, it is conceivable that time-based expectations operate at sensory or perceptual processing stages. Because different targets appear after short and long foreperiods, the corresponding target categories or target features could be primed accordingly (Esterman & Yantis, 2010; Snyder & Foxe, 2010). Expected events would still have a behavioral advantage, but no pre-motor activity should be recorded prior to target detection.

In addition to LRPs, we also investigated oscillatory brain activity. In contrast to ERP analysis, this method also captures induced brain activity that is not phase-locked to the event of interest, making it especially suitable for investigating preparatory brain activity. Particularly oscillations in the alpha frequencies have been identified as a mechanism for gating neural information in perceptual and motor processing (Fox et al., 2016; Klimesch et al., 2007). Higher alpha power indicates inhibition and lower power indicates excitation of task-relevant cortices in either case. We investigated whether time-based expectations induce lateralized alpha activity over the motor cortex, in order to ensure that both phase-locked and non-phase-locked brain activity are considered.

2. Material and methods

2.1. Participants

Twenty volunteers participated in this experiment. One participant was excluded due to data loss during the response registration. A further participant had to be excluded due to strong artifacts in the EEG recordings. Thus, eighteen participants remained for analysis (3 male, 15 female, 22.39 ± 2.38 years, $M \pm SD$).

2.2. Stimuli and procedure

The subjects were seated in a sound-attenuated and electrically shielded chamber (Industrial acoustics GmbH) in front of a translucent screen measuring 73 cm by 53 cm. The stimuli were back-projected onto the screen by a DPL projector (NEC V230X) located outside the chamber that had a resolution of 1280 by 1024 pixels and a refresh rate of 60 Hz. The viewing distance was 70 cm. A chin rest ensured a centered viewing position and a constant viewing distance.

Each trial started with the presentation of a fixation cross in the center of the visual field (Fig. 1). The fixation cross was drawn in black on a uniformly blue background (2.9 cd/m^2). After a foreperiod of either 3 sec ('short foreperiod') or 6 sec ('long foreperiod'), a target stimulus appeared in the center of the screen. The target stimuli extended 3.8° of visual angle and were drawn in yellow (27.6 cd/m^2). Participants categorized stimuli as triangles or circles in a speeded two-alternative forced choice task by pressing a button with the index finger of either the left or the right hand. If the response was given before the stimulus presentation or more than 1 sec after the stimulus onset, a feedback message indicated the response was either too early or too late, and the trial was rejected. Stimuli were shown until the participant responded or until the 1 sec time-out was reached. Successive trials were separated by an inter-trial interval of .8 sec. The mapping of the target stimuli to the response hands was counterbalanced across subjects.

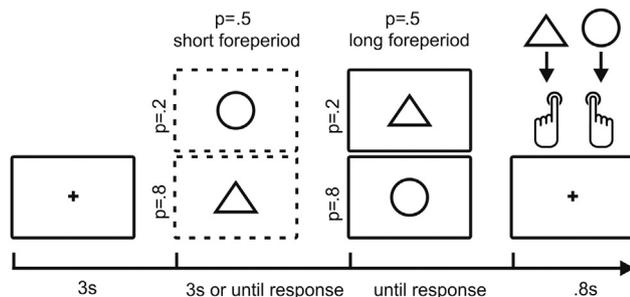


Fig. 1 – A typical trial sequence. A circle or a triangle was presented in the center of the screen after either a short (3 sec, dashed boxes) or long (6 sec, solid boxes) foreperiod. Participants identified the form by pressing a response button with the left or the right hand. The probability of triangles or circles to appear, and thus of either left or right hand buttons as the correct response alternative, co-varied with the length of the foreperiod.

Importantly, the probability that a circle or a triangle would appear as a target – and thus, that a left or a right hand response would be required – co-varied with the length of the foreperiod. The experiment consisted of 320 trials in total, presented in four blocks of 80 trials, 40 with short foreperiods and 40 with long foreperiods, in each block. One of the targets, e.g., the triangle, appeared with a probability of .8 (32 out of 40 trials) after the short foreperiod and with a probability of .2 after the long foreperiod. The other target, in this case the circle, was then presented with a probability of .2 after the short foreperiod and with probability of .8 after the long foreperiod. For half of the participants, the target that appeared with a high probability in the short foreperiod was mapped to a left hand response whereas the target that was shown with a high probability in the long foreperiod was mapped to a right hand response (example depicted in Fig. 1). These participants will be referred to as the 'short left' response group because the more likely target in the short interval required a left hand response. For the other half of the participants the order was reversed ('short right' response group).

The contingencies between foreperiods and targets were learned implicitly during the task execution (Thomaschke & Dreisbach, 2013; Thomaschke et al., 2011). Participants were not informed about the contingencies between foreperiod duration and targets.

2.3. EEG recording and preprocessing

The EEG was recorded from 62 electrodes which were mounted on an elastic cap (EasyCap, Herrsching-Breitbrunn, Germany). Electrodes were placed equidistantly on five rings around electrode Cz. The electrode positions on the vertical and horizontal central lines were identical to those defined in the international 10% system (i.e., electrodes Fpz, AFz, Fz, FCz, Cz, CPz, Pz, Iz, C5, C2, C1, C6; see Oostenveld & Praamstra, 2001). The 10% naming scheme will also be used for the remaining electrodes in the array, according to the closest match. Data were referenced to the vertex electrode during recording. Signals between .1 and 100 Hz were amplified and digitized at a rate of 500 Hz (BrainAmp MR plus, Gilching, Germany), and the impedances were kept below 10 kOhm.

2.4. Data analysis

The first block of trials was considered a learning phase and was excluded from the analysis of the behavioral as well as the EEG data. In addition, trials with too fast or too slow responses (i.e., within the foreperiod or later than 1 sec after stimulus onset) were omitted from all analyses.

2.4.1. Behavioral data analysis

For the analysis of the reaction times, the first trial within each block was discarded, as well as trials with wrong behavioral responses. To further reduce the effect of outliers, the median of the reaction times per condition was used. For the analysis of error rates, the rate of incorrect behavioral responses was computed. 2×2 analyses of variance (ANOVAs) for repeated measures with the factors Foreperiod (short, long) and Target Probability (low, high) were performed. The

generalized eta squared (η^2) is reported as measure of effect size (Olejnik & Algina, 2003). High and low target probabilities refer to frequent and infrequent combinations of targets and foreperiods, respectively.

2.4.2. EEG data analysis

The aim of the study was to investigate how brain activity changes as expectation of an event varies over time. Only trials with long (6 sec) foreperiods could be used for this analysis. The first 3 sec within each trial reflect preparatory brain activity for targets shown after the short foreperiod, while the following 3 sec reflect preparatory brain activity for targets shown after the long foreperiod.

EEG processing was accomplished with custom scripts and the Fieldtrip toolbox (Oostenveld, Fries, Maris, & Schoffelen, 2011) for MATLAB environment (The Mathworks, Inc.). The continuous data was segmented into epochs from -1 to 7 sec relative to the onset of the fixation cross, and pre-cleaned by removing epochs containing electrode or movement artifacts. In a second run, artefactual components related to blinks, eye movements or tonic muscle activity were identified and removed from the pre-cleaned data using an infomax independent components analysis (Delorme & Makeig, 2004). On average, 2.89 (range 1–6) components were removed per subject. Trials with any residual artifacts were identified and removed by visual inspection. Also, trials with incorrect behavioral responses were discarded. On average, 82 trials per subject (range 44–107) remained for the analysis. This number includes both left and right hand responses.

2.4.2.1. LRPs. The raw EEG was low-pass filtered at 5 Hz for the ERP analysis (6-th order, two-pass Butterworth), and baseline-corrected using data -200 to 0 msec relative to the trial onset. Electrodes C3 and C4 were used to compute the LRPs. For each trial and each subject, the ERP at the electrode ipsilateral to the response hand associated with the expected event was subtracted from the ERP at the contralateral electrode. Because a stimulus could occur after a short or long foreperiod, two difference waves were computed per trial. For example, if a target associated with a right button press occurred with $p = .8$ in the short foreperiod, then the difference wave (C3–C4) was computed for the time period between 0 and 3 sec, and (C4–C3) was computed for the interval between 3 and 6 sec of the same trial. In either case, negative values would indicate a stronger negativity at the contralateral compared to ipsilateral electrode, suggesting a preparation of the response hand mapped onto the high probability target. In order to eliminate activity that is unrelated to motor preparation of the response hand, the difference wave was then averaged over left and right hand responses, e.g., over 3 sec segments obtained from short and long foreperiods (e.g., Eder, Leuthold, Rothermund & Schweinberger, 2011). Afterwards the grand mean LRP was computed as the mean of each subject's LRPs. One-sample *t*-tests were applied to assess the deviation of the LRPs from zero amplitude at each sample point (one per 2 msec) within an interval from 0 to 3 sec. For multiple comparison correction, a binomial test was used to compute the probability that the resulting number of significant tests would occur by chance given an alpha error of .05 and 1500 tests. LRP effects were further evaluated by

examining the difference wave at electrodes C3–C4 for the 'short left' and 'short right' response groups separately. The mean amplitudes of the difference waves were compared using an ANOVA with the factors Response group (short left, short right) and Foreperiod (short, long). Further details of the analysis hinged on the outcome of the LRP analysis and are shown in the results section.

Finally, correlations between LRP amplitudes and reaction times were examined, using the LRP amplitude at target onset, 6–6.1 sec relative to trial start. Such peri-stimulus preparatory brain activity is known to be the most predictive for reaction times (Miller, 1998; Thillay et al., 2016). Linear regression analyses were computed across subjects with the z-scored median reaction time as the dependent variable and the z-scored median LRP amplitude as the predictor. The analyses were calculated separately for trials with targets which would appear with high or low probability. A *z*-test was used in order to assess whether the resulting β coefficients differed significantly. The *z* score was calculated as the difference between both β coefficients divided by their pooled standard errors (Cohen, Cohen, West, & Aiken, 2003), and the corresponding *p* was derived from the cumulative density function of a standard normal distribution.

2.4.2.2. TIME-FREQUENCY ANALYSIS. The same EEG segments were used for the time–frequency analysis as for the LRP analysis. The time–frequency decomposition was achieved by convolving filter and data segments in the time domain. To obtain a suitable time and frequency resolution, the filter window length was adapted to contain 7 cycles of the respective center frequency, from 4 to 30 Hz in steps of 1 Hz. Thus, the window length and the frequency resolution decreased linearly with increasing center frequency, from 1.75 sec and .57 Hz at 4 Hz center frequency to .23 sec and 4.29 Hz at 30 Hz center frequency. To sharpen the filter response, the data segment was multiplied with a Hanning taper prior to convolution. Event-related power changes are expressed as the percentage power increase or decrease relative to a baseline period, which was set from -600 to -100 ms relative to the trial onset. In order to identify suitable frequencies for the analysis, the global field power (GFP) was computed for the grand average power for each time and frequency bin within the 6 sec period after trial onset. The GFP is the standard deviation between the channels and can be interpreted as a measure of overall neural response strength (Murray, Brunet, & Michel, 2008). Because lateralized brain responses would be canceled out in the grand mean average across response groups, the GFP was computed separately for 'short left' and 'short right' groups and averaged subsequently.

Relevant electrodes were identified from average power topographic maps for the frequency range identified in the GFP analysis. ANOVAs were computed to compare the power differences between left and right-sided electrodes with the factors Response group (short left, short right) and Foreperiod (short, long), and the mean power differences across both response groups between short and long foreperiods. Finally, z-scored reaction times were regressed on z-scored power at target onset (6–6.1 sec) across participants. Again, the details of this analysis are shown in the results section.

3. Results

3.1. Behavioral data

The reaction time analysis showed faster responses to targets presented after the long foreperiod ($M \pm SD$: 549 ± 52 msec) compared to the short foreperiod (563 ± 53 msec), and faster responses in the high target probability (553 ± 52 msec) compared to the low probability condition (560 ± 52 msec). The differences were reflected in main effects for both factors, Foreperiod: $F(1,17) = 7.59$, $p < .05$, $\eta^2 = .116$, and Target Probability: $F(1,17) = 4.5$, $p < .05$, $\eta^2 = .036$ (Fig. 2). There was no significant interaction between the two factors. A similar but insignificant trend was observed for the error rates. Responses were more accurate after a long foreperiod ($4.54 \pm 3.44\%$ errors) compared to a short foreperiod ($5.98 \pm 3.98\%$), $F(1,17) = 3.88$, $p = .07$, and more accurate in the high probability condition ($4.37 \pm 2.63\%$) compared to the low probability condition ($6.15 \pm 5.15\%$), $F(1,17) = 2.71$, $p = .12$. The factors did not interact significantly either.

3.2. EEG data

3.2.1. LRPs

The data showed a clear LRP during the foreperiod of the upcoming events (Fig. 3A). The LRP amplitude raised shortly after trial onset, reached a maximal negativity at 1.89 sec, and returned to near-baseline levels after the end of the foreperiod. One-sample t -tests on the LRP amplitude were significant at 871 consecutive sample points between 1.154 sec and 2.894 sec after the onset of the foreperiod, $t(17) = -2.11$ to -2.88 , all $p < .05$ (Fig. 3B). The probability of finding 871 or more significant bins in this segment by chance, given 1500 data bins and an alpha of .05, approaches zero in a binomial test ($p < 1.0 \times 10^{-230}$).

To further evaluate this finding, a difference wave was computed from the ERPs at the two central electrodes and

plotted over the whole 6 sec segment (C3–C4, see Fig. 3C). Positive values indicate a stronger negativity at the right electrode compared to the left one, suggesting a motor preparation of the left hand. Negative values indicate the opposite relation and therefore suggest a stronger motor preparation of the right hand. The difference waves were computed separately for ‘short left’ (black line) and for ‘short right’ (blue line) response groups. Evidently, the difference waves changed polarity between the short and the long foreperiod, with a deflection point shortly after the expiration of the short foreperiod. Moreover, the polarity was reversed between response groups. Whereas the difference wave for the ‘short left’ response group showed a positive amplitude during the short foreperiod and a negative amplitude during the long foreperiod, the ‘short right’ group showed a negative amplitude in the short foreperiod and a positive amplitude in the long foreperiod. Topographic maps indicate that this lateralization occurred focally at the investigated electrodes C3 and C4 for both groups (Fig. 3D).

To test this pattern of results, the amplitudes of the C3–C4 difference waves were averaged within the previously identified LRP time range, i.e., within 1.154–2.984 sec in the short foreperiod and within 4.154–5.984 sec in the long foreperiod. The data were then compared in a 2×2 ANOVA with Foreperiod (short, long) as a within subject factor and Response Group (short left/long right, short right/long left) as a between-subject factor. The expected interaction between the factors Foreperiod and Response Group was highly significant, $F(1,16) = 17.62$, $p < .001$, $\eta^2 = .13$. The amplitude change between short and long foreperiods was significant or marginally significant in both response groups when tested separately, short left: $F(1,8) = 13.22$, $p < .01$, $\eta^2 = .19$; short right: $F(1,8) = 4.48$, $p = .07$, $\eta^2 = .06$. Furthermore, the mean amplitudes of the difference waves for short and long foreperiods were compared and contrasted for each response group separately. The difference was insignificant in both cases, short left: $t(8) = -.26$, $p > .7$; short right: $t(8) = .07$, $p > .9$. Thus, readiness potentials had about the same size in the early and late foreperiods.

3.2.2. Time–frequency analysis

The GFP was computed in order to identify suitable time and frequency ranges for the analysis. There was a strong GFP increase between 9 and 12 Hz, emerging shortly after stimulus onset and remaining over the whole 6 sec segment (Fig. 4A). No comparable increase in GFP was observed in other frequencies. To identify further relevant electrodes for the analysis, topographic maps of the mean 9–12 Hz power were computed separately for each response group and for short and long foreperiods (Fig. 4B). In either case, the power modulations occurred focally at posterior central electrodes (CP1, CP2, CPz, Pz). A visual inspection of the topographies showed a slightly higher power at right-compared to left-sided electrodes, but no difference in lateralization between response groups. As a test, the average 9–12 Hz activity at electrodes CP1–CP2 in the short foreperiod (1.15–2.98 sec) and long foreperiod (4.15–5.98 sec) were contrasted between response groups in a 2×2 ANOVA using the same time range and statistics as in the LRP analysis. There was no interaction between the factors Response Group and Foreperiod,

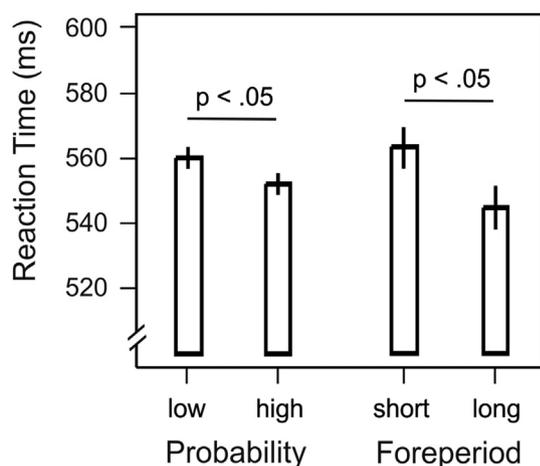


Fig. 2 – Median reaction times show faster responses to targets which appeared with a high compared to a low probability, and faster responses after long compared to short foreperiods.

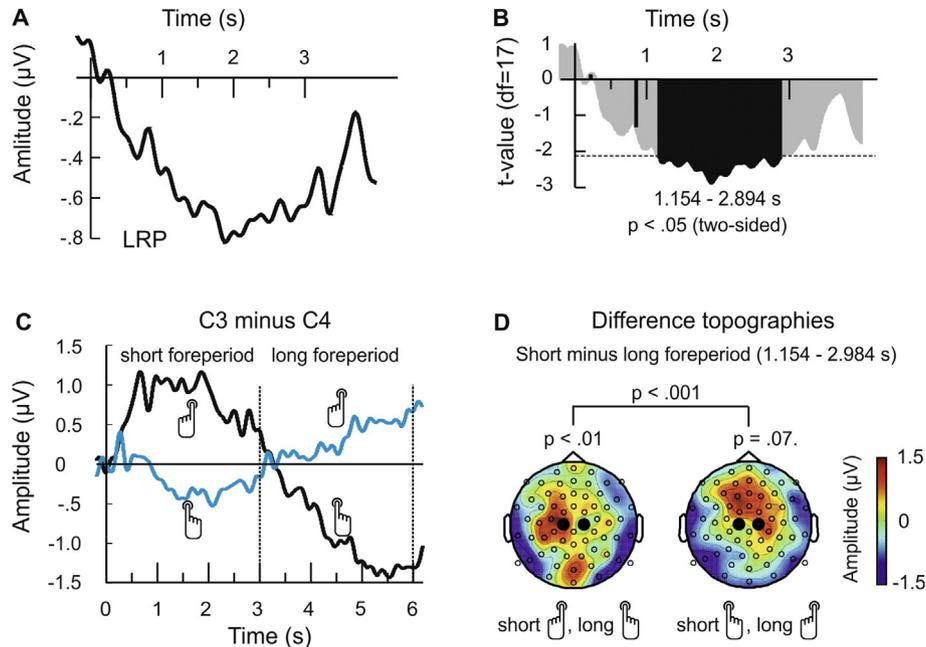


Fig. 3 – Results for the lateralized readiness potentials (LRP). A LRPs at electrodes C3 and C4 in the 3 sec interval preceding targets presentation, averaged over short and long foreperiods. B The LRP amplitude was significantly below baseline for a 1.8 sec interval prior to the expected event. Black coloring indicates significant sample points, obtained from one-sample t-tests. C Differences in potentials (C3–C4) display an interaction between the factors Foreperiod and Response group. Blue coloring indicates participants belong to the response group which was required to answer with the right hand in the short foreperiod and with the left hand in the long foreperiod, black coloring indicates the reversed arrangement. D Topographical differences for the waveforms shown in subplot C. Electrodes C3 and C4 are marked in black.

$F(1,16) = .3, p = .59$, and no effect of Foreperiod when investigating the response groups separately, both $|t(8)| < .93$, all $p > .3$. Thus, the 9–12 Hz power was not lateralized like the ERPs.

Because the response group was not a factor, the data of both groups were merged for further analysis and then averaged over the previously identified electrodes CP1, CP2, CPz and Pz. The power time course showed a continuous increase from baseline levels with a broad peak in the short foreperiod, between 1 and 3 sec after trial onset. The power then

continued to steadily decrease throughout the long foreperiod (Fig. 4C). There was no change in topography between the conditions. As a formal test of power decrease over time, the power between 9 and 12 Hz was first averaged over the selected electrodes (CP1, CP2, CPz and PZ). Then separate averages were obtained for the time ranges 1–3 sec (short foreperiod) and 4–6 sec (long foreperiod) and compared in a one-way ANOVA with the factor Foreperiod (short, long), which revealed a main effect for that factor, $F(1,17) = 9.4, p < .01, \eta^2 = .05$.

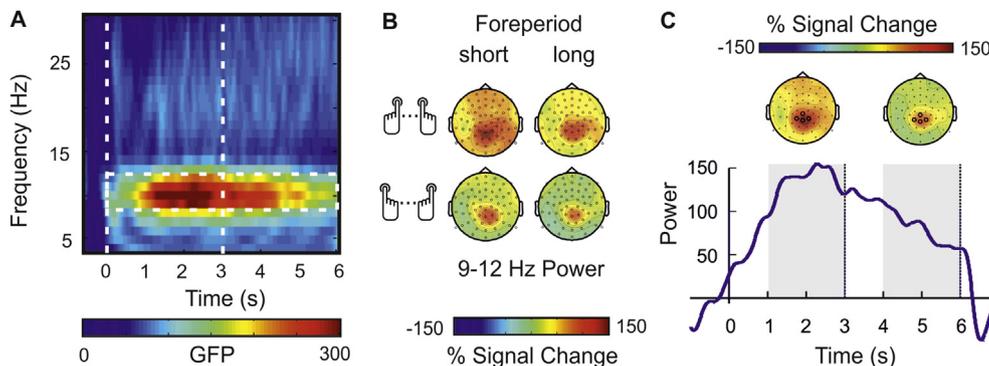


Fig. 4 – Results of the time–frequency analysis. A Global field power indicating a strong response in alpha frequencies (9–12 Hz) across the whole time course. B Mean alpha power in short and long foreperiods contingent on the response group. C Alpha power waveform, averaged over central electrodes. Shaded areas mark time ranges used for statistical comparison, see text for more details.

3.2.3. Correlations with behavior

The LRP analysis revealed a temporally specific motor preparation that would favor responses to the more probable target in each foreperiod. Lower LRP amplitudes, suggesting such relevant motor preparation, should then accompany lower reaction times for more probable targets and higher reaction times for less probable ones. To test that prediction, linear regression analyses were performed on the median reaction times and median LRP amplitudes across participants. Both variables were z-scored. Observations exceeding $|z| = 2.5$ for either variable were excluded from the parameter estimation, one observation for highly probable targets and two observations for less probable targets. The regression analysis showed only an insignificant positive relation between LRP amplitude and reaction time for highly probable targets, $\beta = .13$, $t(15) = .33$, $p = .75$, but a strong negative association between these measures for less probable targets, $\beta = -.63$, $t(14) = -3.04$, $p < .01$. Thus, as expected, high (i.e., more negative) LRP amplitudes were associated with longer reaction times in this condition (Fig. 5). A z-test on the β values confirmed that the difference between less probable and highly probable events was significant, $z = 1.66$, $p < .05$ (one-sided).

Reaction times were also regressed on the 9–12 Hz power at stimulus onset. Both variables were z-scored and observations exceeding $|z| = 2.5$ for either variable were excluded. There was no effect in this analysis though, $\beta = -.12$, $t(15) = -.3$, $p = .77$.

4. Discussion

When events occur at predictable points in time, observers form implicit time-based expectations that guide future behavior. Unlike explicit cues, implicit temporal cues do not direct attention to a specific quality of upcoming events. It was therefore unknown which component of the event processing, from sensation and perception to action, is facilitated by time-based expectations. We investigated the role of motor preparation in time-based expectations in a simple EEG experiment, where two visual objects were presented after a characteristic short or long foreperiod, and a left or right hand response was required to indicate the object category. If time-based expectations rely on motor preparation, then

lateralized readiness potentials should have appeared within the short and long foreperiod, favoring responses to the more likely object. Alternatively, if time-based expectations rely on perceptual preparation, then a behavioral advantage but no LRP differences should have been observed for expected compared to unexpected events.

Responses were faster and more accurate for frequent compared to infrequent combinations of events and foreperiods, that is, for events that occurred at an expected compared to an unexpected point in time (Schröter, Birngruber, Bratzke, Miller, & Ulrich, 2015; Thomaschke & Dreisbach, 2013, 2015). At the same time, we found readiness potentials during the whole course of the trial. After the short foreperiod, the readiness potential changed polarity, as did the response preparation for the left or right hand. The change took place at exactly the point in time that marks a reversal of the event probability. Thus, participants were continuously prepared to respond to the respectively more likely target contingent on time. Moreover, we found that the amplitude of the LRP was associated with the performance: Across participants, high (negative) LRP amplitudes impaired responses to unexpected events but not to expected events. Altogether, the results strongly suggest that temporal cues prepare reactions to expected or unexpected events.

A popular strategy for examining reaction-time effects with LRPs is to determine their onset relative to the preceding stimulus (S-LRP) or to the following response (R-LRP). The resulting latencies can be interpreted as the time required for the response selection and motor processing for the task at hand, respectively (Eder, Leuthold, Rothermund, & Schweinberger, 2011; Leuthold, Sommer, & Ulrich, 1994). Such analysis could not be applied to the present study because there was no objective onset time for the second foreperiod, which is the relevant cue for the overt response. We will therefore focus on a discussion of the relation between LRP amplitudes and reaction times.

Interestingly, a relation between reaction times and LRP amplitudes was only manifest for unexpected events, i.e., when the prepared response and the required response were incongruent. Congruency has often an asymmetric effect on performance, such that the unfavorable impact of incongruent information is stronger than the favorable effect of congruent information (Lindsay & Jacoby, 1994; for an overview see; MacLeod, 1991). This seems to be true also for the

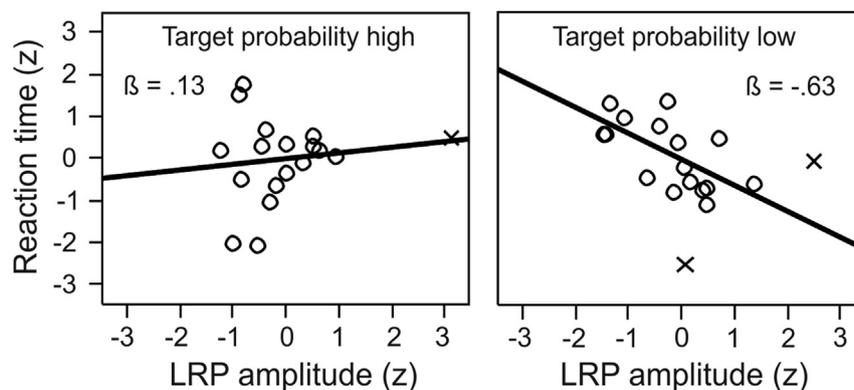


Fig. 5 – Linear relationship between the z-scored reaction time and the LRP amplitude across subjects. Crosses mark excluded outliers.

present study. Our results show that the response pre-activations imposed a processing disadvantage for unexpected events rather than a processing advantage for expected events. A possible explanation is that those events that were unexpected in the long foreperiod are the same events that were expected in the preceding short foreperiod. The responses therefore had to be inhibited in the earlier part of the trial (Kingstone, 1992). This inhibition might have carried over to the second foreperiod, and hindered responses to the then unexpected events. A similar inhibition would not occur for responses to events only expected later on. Hence, the relation between response activation and overt reaction differs between the types of event sequences.

Importantly, our paradigm emphasized motor preparation while a perceptual preparation, e.g., towards features or categories of the objects, would be difficult. The paradigm did not induce a specific EEG correlate for perceptual preparation comparable to the LRP in the motor domain. We can therefore not conclude that time-based expectations rely exclusively on motor activity. Temporal expectation in general can facilitate processing at various stages, from perception to action, depending on the task difficulty (Correa, Lupiáñez, Madrid, & Tudela, 2006; Seibold & Rolke, 2014). Similarly, time-based event expectations might rely more on perceptual than on motor preparation in tasks in which this is more efficient. The present data does not preclude this possibility. However, the data do show that motor preparation is at least one important factor in time-based expectations.

A further interesting finding is that participants responded faster and more accurately if an event occurred after a long compared to a short time interval. This so-called ‘variable foreperiod effect’ is well investigated, and is thought to reflect the increasing conditional probability of an event given that the event has not occurred yet (Los, 2013; Vallesi, McIntosh, Shallice, & Stuss, 2009). For example, in the present experiment the probability that a target would appear after the long foreperiod is $p = .5$ at trial start, but $p = 1$ after the shorter foreperiod has elapsed. Previous research suggests that such event probabilities are monitored in dorsolateral or dorso-medial prefrontal cortices (Laubach, Caetano, & Narayanan, 2015; Vallesi et al., 2009), which modulate the excitability of the corticospinal system in a top-down fashion (van Elswijk, Kleine, Overeem, & Stegeman, 2007). Our data showed a corresponding modulation of alpha power at posterior central electrodes near the motor cortex, which peaks in the short foreperiod and decreases over the remainder of the course of the trial. In perceptual processes, high alpha power in the motor domain is thought to reflect inhibition of currently task-irrelevant cortices (Brinkman, Stolk, Dijkerman, de Lange, & Toni, 2014; Jensen & Mazaheri, 2010; Pineda, 2005; Pineda et al., 2013). While the LRPs represent effector-specific motor preparation, high alpha power might signify an overall response inhibition for both effectors. Together the EEG results suggest that effector-specific motor responses were prepared, as seen in the LRP, but inhibited during the majority of the trial course, as seen in the alpha power. They became disinhibited at time points where an event would likely occur. This is evident at the 6 sec boundary where a strong alpha power decrease relative to peak levels (~2 sec) was observed. A less prominent decrease occurred also prior

to the 3 sec boundary. This might reflect a release from inhibition towards the end of the first foreperiod, but also might constitute an initial decrease towards the 6 sec boundary if participants underestimated the length of the short foreperiod. In any case, the alpha power was high if the probability of a target appearing was low. Premature reactions to unexpected events could possibly be prevented this way (Correa, Triviño, Pérez-Dueñas, Acosta, & Lupiáñez, 2010).

Time-based expectations are established if specific events frequently occur at specific time points. They can thus be considered a variant of implicit timing, where temporal regularities in the trial structure are extracted *en passant* and facilitate responses to future events (Coull & Nobre, 2008). Tasks with an implicit temporal structure often recruit action-related cortices (Triviño et al., 2016), even if no motor response is required (Schubotz & von Cramon, 2001). Such time-contingent motor excitation cannot explain our results, though. The crucial aspect of our paradigm is that the temporal cue referred to different events that required different responses. A general motor excitation at the expected event onsets (i.e., after the short or long foreperiods) would facilitate the correct as well as the incorrect response and would thus not enhance performance. A similar argument holds for sensory excitation. Visual stimuli occurring at expected time points produce larger P1 amplitudes of the event-related EEG potential compared to those shown at unexpected time points (Correa et al., 2006; see also; Cravo et al., 2013). This suggests that the incoming sensory information is amplified if it is expected at a specific time point (Hillyard, Vogel, & Luck, 1998; Luck, Woodman, & Vogel, 2000). However, an overall increase of sensory gain would not speed up the selection of specific stimulus features and thereby the categorization of triangles or circles in the present study.

The presented LRP results are in agreement with the outcome of a previous behavioral study. Thomaschke and Dreisbach (2013; cf. Thomaschke et al., 2016) used different mappings between foreperiods and response fingers and found an effect of time-based expectations only when the foreperiod was correlated with specific effectors. The authors concluded that time-based expectations facilitate action to upcoming visual events. It was however unclear whether time-based expectations operate on cognitive representations of actions, or whether they directly prepare for motor activity (Cavina-Pratesi et al., 2006; Johnston & Everling, 2006). Our findings show, for the first time, that time-based expectations do indeed prepare directly for action. We cannot preclude that time-based expectations are additionally governed by perceptual mechanisms. However, the prominent LRPs observed during the foreperiods, as well as the correlation of the LRP amplitudes with performance, strongly support a critical role of motor preparation.

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