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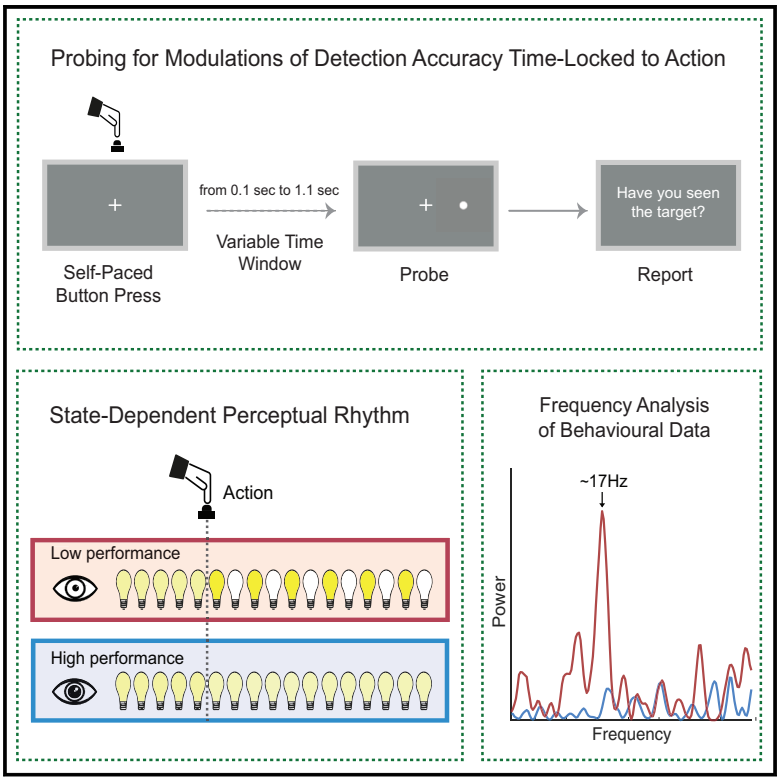
Performance modulations phase-locked to action depend on internal state

Graphical abstract



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In brief

Biological sciences; Neuroscience; Cognitive neuroscience

Highlights

- No action-related rhythmic performance modulation found when pooling all data
- Both trial and subject splits reveal ∼17 Hz modulation in random effect tests
- ∼17 Hz modulation in trials and in subjects with low engagement or high criterion
- Internal states affect action-related modulations in the beta-frequency range

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Performance modulations phase-locked to action depend on internal state

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SUMMARY

Previous studies have shown that perceptual performance can be modulated at specific frequencies phase-locked to self-paced motor actions, but findings have been inconsistent. To investigate this effect at the population level, we tested 50 participants who performed a self-paced button press followed by a threshold-level detection task, using both fixed- and random-effects analyses. Contrary to expectations, the aggregated data showed no significant action-related modulation. However, when accounting for internal states, we found that trials during periods of low performance or following a missed detection exhibited significant modulation at approximately 17 Hz. Additionally, participants with no false alarms showed similar modulation. These effects were significant in random effects tests, suggesting that they generalize to the population. Our findings indicate that action-related perceptual modulations are not always detectable but may emerge under specific internal conditions, such as lower attentional engagement or higher decision criteria, particularly in the beta-frequency range.

INTRODUCTION

The brain entails many rhythms, which in turn entail excitability fluctuations of the participating neurons. This likely influences the respective neuronal processing, such that processing is modulated by the phase of the rhythm. Since behavior depends on neuronal processing, these rhythms can become directly visible in behavior. This can be investigated in at least two ways. First, by recording brain activity and showing that the phase of a rhythm modulates detection or discrimination performance.[1] Second, by resetting a brain rhythm and showing frequency-specific modulations of task performance phase-locked to the reset. As a reset, an external event can be used, such as a flash or a sudden sound, which probably acts by resetting the phase of some internal rhythms in a bottom up fashion.[2,3] Alternatively a self-paced motor action can be used, such as an arm movement, a saccade, or a button press.[4–6] This may also act by resetting the phase of some internal rhythms, either by a corollary discharge signal sent from motor to sensory areas, or by sensory re-afference. Additionally, a motor action may reveal the phase of some internal rhythms modulating the likelihood of initiating that movement.

Recently, there was a debate about reproducibility of psychophysics studies reporting such modulations[7–9] and about the correct use of analysis methods in the field.[10–13] The fact that different studies applied different analysis methods and statistical tests makes the comparison difficult. Moreover, published studies show substantial discrepancy with regard to frequency and strength of effects. For example theta- or alpha-band centered modulations have been reported in different studies.[14] Some of the variability has been addressed as a consequence of differences with regard to task difficulty,[15] background luminosity,[5] and attention.[16,17]

Intriguingly, spontaneous slow fluctuations between brain states characterized by different oscillatory signatures have been described.[18] This might well lead to different rhythms transpiring into behavior, within one participant at different times (assuming that the different states are alternating during the experimental session) or across different participants with different biases to one or the other state.

The debate about reproducibility might benefit from a study that uses a basic, simple paradigm in a relatively large sample size, and a statistical approach allowing an inference on the

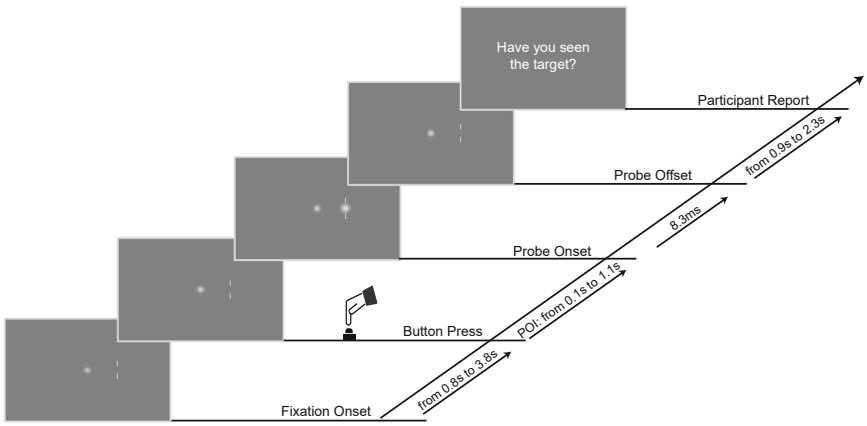

Figure 1. Task paradigm

The trial started with the display of a fixation point and two fiducial lines on a gray background. Participants were instructed to perform a self-paced button press in a time window ranging from 0.8 to 3.8 s after the start of the trial. Following the button press, a probe appeared in 90% of the trials. Probe onset intervals (POIs) ranged from 0.1 to 1.1 s. After an additional delay, the question "Have you seen the target" appeared on the screen, and participants responded "Yes" or "No" on a keypad.

population. Therefore, we performed a study on 50 participants, using a self-paced button press followed by a detection task.

To our surprise, averaging our data over all trials of all participants, we found no significant frequency-specific modulation of perceptual performance phase-locked to the motor action. However, when we split trials based on performance in neighboring trials, we found an action-related modulation centered at ≈17 Hz. When we split trials based on the performance in the preceding trial, we found that trials following a "miss" showed an action-related modulation at ≈17 Hz. Finally, when we split participants based on their false-alarm rate, we found that participants with no false alarms showed an action-related modulation at ≈17 Hz. A 17 Hz behavioral modulation suggests an underlying neuronal beta rhythm.

RESULTS

Participants performed a self-paced button press, followed by a detection task on a probe that was presented at variable probe onset intervals (POIs), spanning from 0.1 to 1.1 s, after the button press (Figure 1). The probe's contrast was adjusted with a staircase procedure such that performance was maintained close to 50%. For a detailed performance analysis see Figure S1.

Analysis of the aggregate data

Each trial provided a "hit" or a "miss", referred to as behavioral response value (BRV). We analyzed all trials of all participants, testing for the hypothesized modulation of hit rate that was phase-locked to the reset event, here the button press.[11] We calculated a hit rate time course (HRTC) for each participant by convolving the BRVs, which were aligned accordingly to their POIs, with a Gaussian kernel. Each HRTC was then linearly detrended, and the detrended HRTCs of all participants were averaged to give the mean HRTC, shown in Figure 2A. The phase-locking spectrum was estimated by means of a single-trial least square spectral analysis (stLSSA) applied to the trials of each participant separately, after linear detrending and Hann tapering.[11] In this way we obtained a complex spectrum per participant, and we then averaged the spectra of all participants. Lastly, we took the absolute values of the average spectrum, and we squared it to obtain the power.

To determine significance, we first performed a fixed-effects non-parametric statistical test. To do so, we compared the values of the spectrum of the observed data to a distribution of values obtained by shuffling 5000 times the POIs of each participant and repeating the same analysis performed for the observed data. The observed spectrum was normalized by the mean of the spectra of the permuted data, for a better comparison with the following analysis. No frequency bin reached significance ($p < 0.5$) after a max-based multiple comparison correction (Figure 2B).

We then performed a random effects statistical test. To do so we calculated for each participant a bias-estimate spectrum (see STAR Methods). We then performed a paired t-test to compare the observed spectra and the bias-estimate spectra across participants, thereby obtaining the observed t-value spectrum (Figure 2C). These t-values where then compared to a distribution of t values obtained after randomly exchanging in each participant the observed spectra and the bias-estimate spectra. No frequency bin reached significance ($p < 0.5$) after a max-based multiple comparison correction.

Task epochs with lower average performance show ≈17Hz hit rate modulation

It is known that the brain switches between different states over time.[19] For example, states of relatively strong theta and weak alpha rhythmicity in sensory areas are a signature of strong attentional engagement.[18] Moreover it is known that participants do not sustain a constant level of attention during a task, but they repeatedly drift into mind wandering.[20] We hypothesized that our participants may have gone through different states, for example of higher and lower attentional engagement. We reasoned that different levels of attentional engagement would have differently affected task performance. Therefore, we quantified performance for neighboring trials, referred to as local performance, and investigated effects of local performance on action-related modulation. Periods in the session where the local performance was higher than the overall performance were referred to as "*high-performance epochs*" and those where it was lower as "*low-performance epochs*" (see STAR Methods). We split the trials based on whether they had occurred in high- or low-performance epochs, and repeated the above analyses for those two groups of trials (Figures 3A–3C). *Low-performance epochs* resulted in significant action-related modulation at ≈17 Hz, which

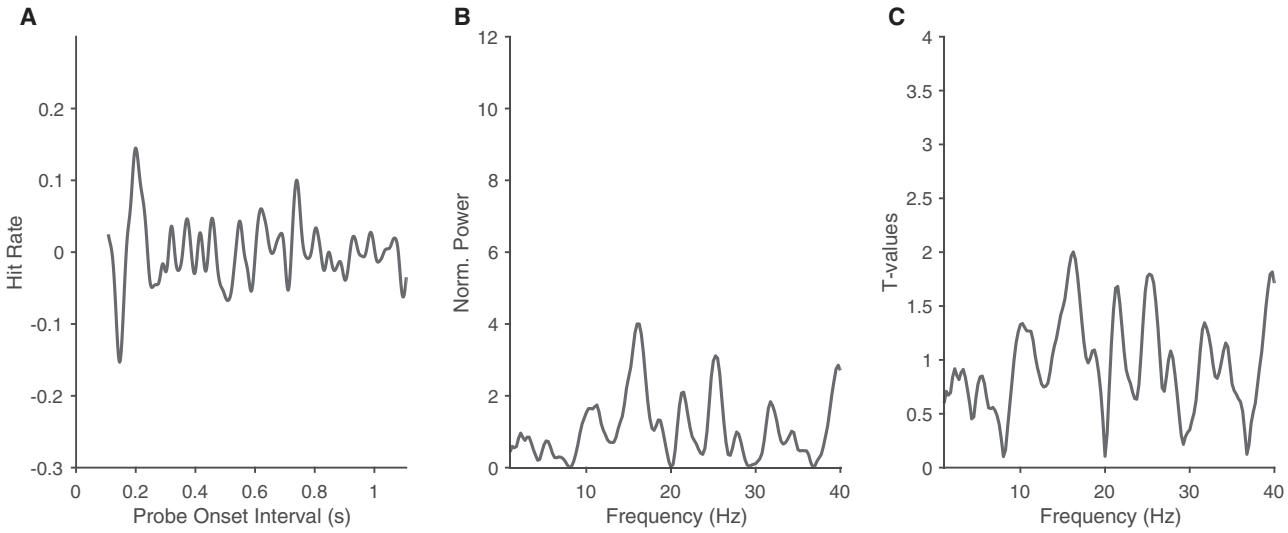

Figure 2. Spectral analysis of the pooled data (*N* = 50 participants)

(A) Mean hit rate time course obtained by averaging the linearly detrended hit rate time courses of each participant.

(B) Power spectrum obtained by squaring the absolute values of the average over the individual participants' spectra.

(C) T-value spectrum resulting from paired t-tests comparing the observed spectra and the bias-estimate spectra across all participants.

was significant both for a fixed-effects (Figure 3B) and for a random effects test (Figure 3C). For high-performance epochs, there was no such effect. A direct random effects test between low-performance and high-performance epochs did not show a significant difference.

In a separate analysis, we confirmed that low-compared to high-performance epochs had lower hit rate (Figure 4A, $p < 0.001$). Intriguingly, low-compared to high-performance epochs also had smaller pupil diameter (Figure 4B, $p < 0.001$) and higher microsaccade rate (Figure 4C, $p < 0.001$). Lower hit rate, smaller pupil diameter and higher microsaccade rate are consistent with states of lower attentional engagement.[21–23] However, note that by directly splitting trials based on pupil diameter we did not find any significant modulation (see Figure S2).

Trials following a missed detection show ≈17 Hz modulation

A recent study showed that the dynamic of rhythmic sampling in a given trial is influenced by the stimulus identity in the previous trial.[24] The authors speculated that this is due to different predictions or expectations induced by the previous stimulus. Inspired by this study, we decided to split our trials based on the previous trial's performance. We therefore divided our trials in two groups based on the performance history, and we referred to them as *"trial -1 hit"* and *"trial -1 miss"* (Figures 3D–3F; the first trial of each block was excluded as it had no immediately preceding trial). The *"trial -1 miss"* group showed significant action-related modulation at ≈17 Hz, which was significant both for a fixed-effects (Figure 3E) and for a random effects statistical approach (Figure 3F). For the *"trial -1 hit"* group, there was no such effect. A direct random effects test between the *"trial -1 hit"* and *"trial -1 miss"* groups of trials was significant at ≈16 Hz.

In a separate analysis, we found that "trial −1 miss" compared to "trial −1 hit" trials had lower hit rate (Figure 4D, $p < 0.001$). Intriguingly, "trial −1 miss" compared to "trial −1 hit" trials also had smaller pupil diameter (Figure 4E, $p < 0.001$) and higher microsaccade rate (Figure 4F, $p < 0.001$). As mentioned above, this is consistent with states of lower attentional engagement.

Participants with no false alarms show ≈17 Hz hit rate modulation

Finally, we explored the possibility that the number of false alarms (FAs) in each participant may correlate with the presence or absence of the ≈17 Hz modulation. We therefore split participants based on the total number of FAs (Figures 3G–3I). Participants who performed one or more false alarms constituted the group referred to as "*some FA"* (26 participants), and participants who did not perform any false alarms constituted the group referred to as "*no FA"* (24 participants). The "*no FA*" group showed an action-relation modulation at ≈17 Hz, which was significant both in a fixed-effects (Figure 3H) and in a random effects (Figure 3I) statistical test. The "*some FA"* group showed no such effect. A direct random effects test between the two groups revealed no significant difference.

Note that the results presented in Figure 3 contained also trials in which the probe was presented shortly after a microsaccade occurred. In a control analysis we removed all trials containing a microsaccade in the 100ms before probe onset, and we could replicate the original findings (see Figure S3).

DISCUSSION

In summary, when all participants and all trials were combined, the self-paced button press was not followed by frequency-specific modulations of perceptual performance phase-locked to the action. However, when participants or trials were split based

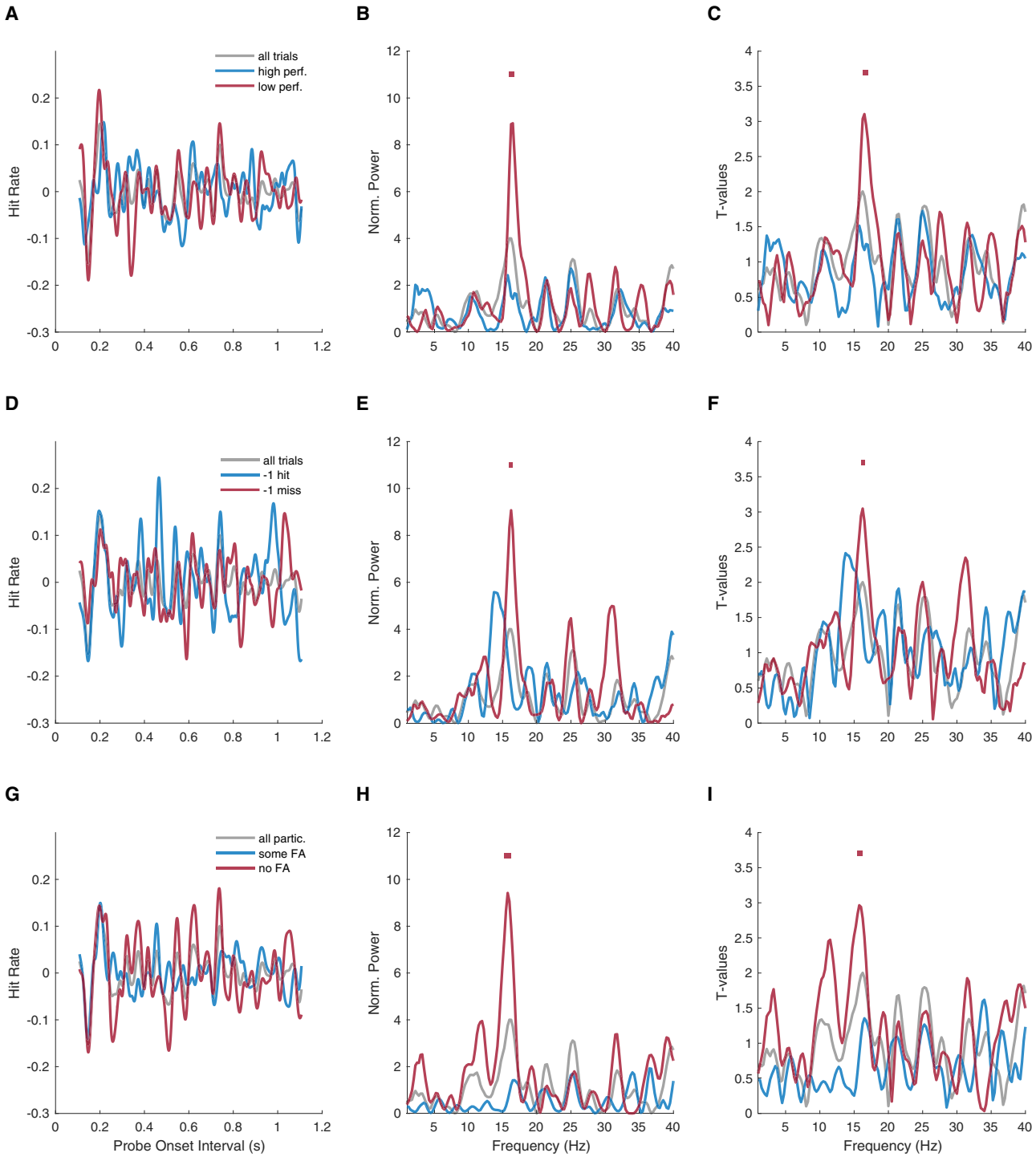

Figure 3. Spectral analysis of subsets of trials or participants

(A) Mean ATC, calculated separately for the trial group "low performance epochs" (red line), "high performance epochs" (blue line), and for all trials pooled (gray line). Spectra were computed and averaged across all participants (N = 50), with trial counts per condition being 9825 and 7791 for low and high performance epochs respectively.

(B) Using the color code of (A), spectra show results for fixed-effects test. Power values are derived from complex-domain averages across participants, where individual participants' complex spectra were averaged before computing power. Significant frequency bins are marked above the spectra in the corresponding color.

(legend continued on next page)

on behavioral performance, action-related modulation emerged. When trials were split based on hit rate in neighboring trials, the subset of trials with low hit rate showed a ≈17 Hz modulation. Similarly, when trials were split based on whether the previous trial was a miss, the subset of trials following miss trials showed a lower hit rate and a ≈17 Hz modulation. For both of these trial splits, the trial subset with lower performance also showed smaller pupil size and higher microsaccade rate. Finally, when participants were split based on false-alarm rate, the subset of participants without false alarms showed a ≈17 Hz modulation.

Several seminal studies have reported periodic modulations of task performance aligned to a voluntary motor action, such as an arm movement,[4,25] a button press,[5,26,27] or a saccade.[28–30] Other studies have reported performance modulations after a sensory event, such as a visual flash[2,31,32] or an auditory input.[33–35] These studies are based on the assumption that sensory events reset, and motor actions reset and/or reveal the phase of brain rhythms, allowing the experimenter to align trials to that event.

In contrast to our initial hypothesis based on these findings, we did not find any significant hit rate modulation after button press in our pooled data. This result adds to other recent reports of inconclusive and null findings[8,36,37] and it is in line with the general revision happening in the field.[38] However, this result does not question the validity of the studies implementing similar paradigms,[5,26,27] because of differences in the task design. For example, we used a detection task with small stimuli presented in the periphery, instead of a discrimination task with larger stimuli presented in the fovea.

We explored the possibility that a modulation was present in a subset of trials and participants, by performing a post-hoc splitting of the data. This revealed significant phase locking at ≈17 Hz in trials occurring during task epochs characterized by lower mean performance, in trials occurring after a missed detection, and in participants that did not commit false alarms. The significant frequency bins at ≈17 Hz were part of a peak that stood out clearly in the spectrum, which is suggestive of an underlying beta-band rhythmicity. Note that spurious peaks in such phase-locking spectra can arise by a combination of higher-order detrending, amounting to high-pass filtering, with binning, amounting to low-pass filtering.[11] Therefore, we used neither higher-order detrending nor binning. Furthermore, when these data analysis steps produce spurious peaks, they are typically at the low end of the spectrum, whereas we found peaks consistently at ≈17 Hz.

Typical modulation frequencies in previous studies were lower in frequency, in the theta or alpha range. The finding of a modulation in the beta range however is in line with recent reports. Veniero et al.[39] applied a TMS pulse on FEF while participants were performing a motion discrimination task, and immediately after the TMS pulse, task performance was modulated at ≈17 Hz. In the same study, the TMS pulse on FEF was shown to reset the phase of the low-beta oscillations recorded by the EEG occipital channels. A similar reset of beta oscillations may have happened in our experiment due to a corollary discharge in FEF, or related prefrontal/premotor region, linked to the button press. Other studies stressed the importance of beta oscillation for attentional processes in FEF[40] and area V4.[41]

Bell et al.[24] also reported a behavioral modulation in the beta range. Specifically, they show a modulation of decision bias in a discrimination task of gender of androgynous faces, and the frequency of this modulation was either 14 Hz or 17 Hz depending on the identity of the previous stimulus. The fact that the previous stimulus influenced the hit rate modulation in the following trial is in line with our findings where the previous response influenced the modulation.

Other studies suggested that the frequency of rhythmic sampling may depend on different factors, such as task difficulty[15] and the attentional demands during the task,[42] which is in line with our interpretation that the action-related modulation might be related to attentional engagement. An additional explanation for the different frequencies reported in different studies is that different periodic modulations coexist in the brain, and the brain circuits recruited to perform a specific task, or reset by a specific event, may be under the influence of one or the other process.[14]

We would like to offer two potential interpretations of the results of the analyses that split the data. The first interpretation pertains to the trial splits within participants and states that the presence of the ≈17 Hz modulation is a signature of lower attentional engagement in the task. Task epochs with lower performance may be a result of disengagement from the task, either because of fatigue, or mind wandering, or a combination of both. Trials following a missed detection were more likely to be a miss again, possibly because a state of lower attentional engagement was carried over from the previous trial. Visual attentional engagement in the absence of visual stimulation, as in the pre-probe period here, has been linked to reduced activity in the beta band, which includes the ≈17 Hz band found here.[43] The pupil and microsaccade data corroborate this interpretation, showing smaller pupil diameter and higher microsaccade rate in those trial subsets that contain the ≈17 Hz modulation. Small pupil diameter is known to be correlated with reduced arousal and locus coeruleus activation.[19]

An alternative interpretation pertains to the trial splits within participants and to the participant split, and it states that the presence of the ≈17 Hz modulation is a signature of a more conservative response criterion, i.e., a bias to report the absence of the target. Task epochs with lower performance may represent a higher criterion, leading to a higher proportion of misses. Trials following a miss were more likely to be a miss again, because a state of more conservative criterion was carried over from the previous trial. Participants with no false alarms performed the task with a higher criterion, which kept them from issuing false alarms. Beta band activity has been linked to mechanisms that maintain an existing state, or "status quo",[44–46] which might be related to a relative resistance against reporting a probe,

(C) Same as (B), but for random effects test.
(D–F) Same as A-C, but for the trial split indicated in D, namely "trial −1 miss" (red, 7502 valid trials), "trial −1 hit" (blue, 6779 valid trials), and all trials (gray).
(G–I) Same as A-C, but for the participant-split indicated in G, namely "no FA" (red, 24 participants), "some FA" (blue, 26 participants), and all participants (gray).
Statistical significance assessed at $p < 0.05$, corrected for multiple comparisons.

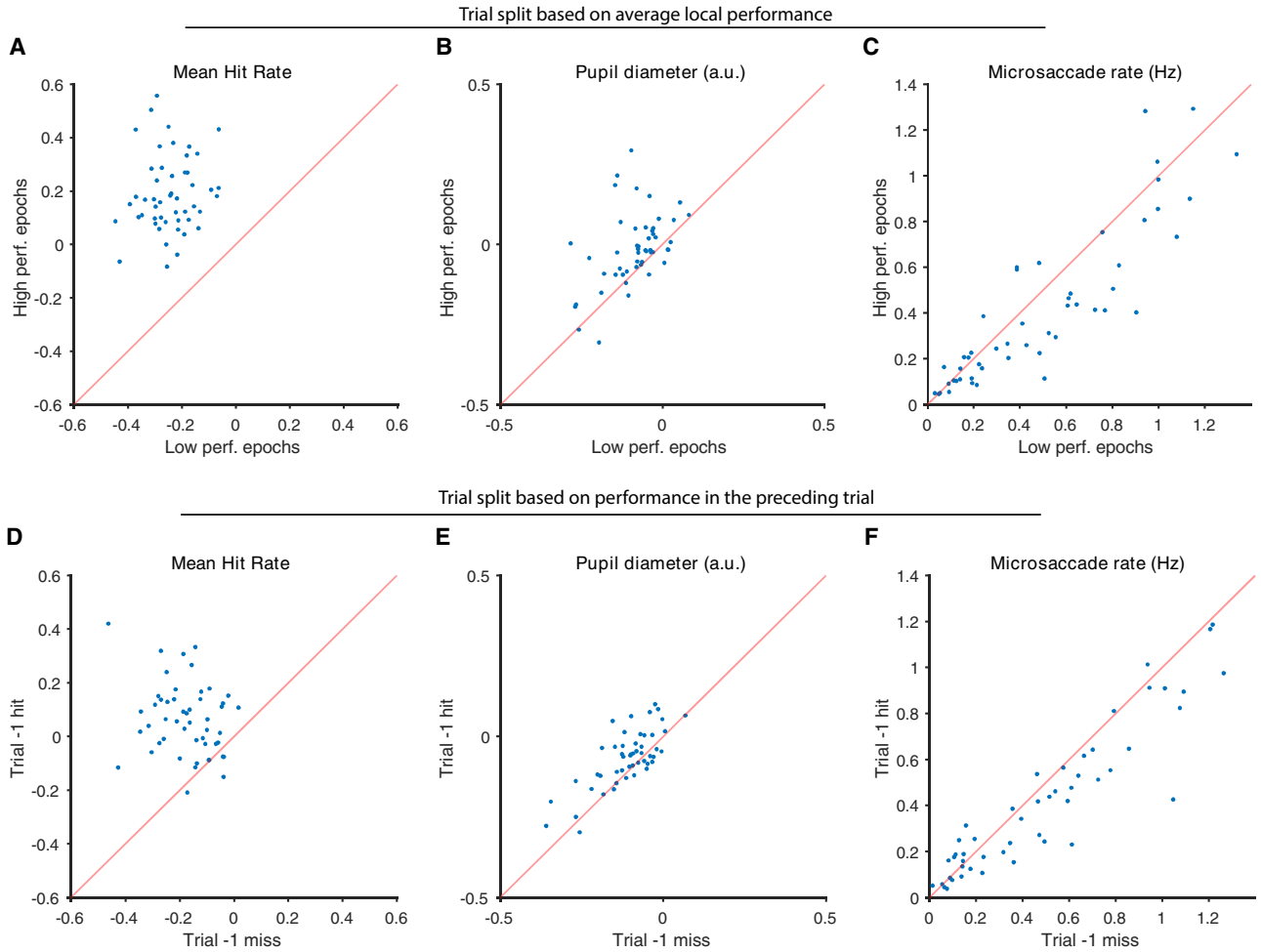

Figure 4. Characterization of subsets of trials

(A) Scatterplot of mean hit rate for trials from "*low performance epochs*" versus "*high performance epochs*"; each dot corresponds to one participant ($N = 50$). Diagonal unity line represents equal performance between conditions.

(B) Same as A, but showing mean pupil diameter.

(C) Same as A, but showing microsaccade rate.

(D–F) Same as (A–C), but for "trial −1 miss" versus "trial −1 hit" trials.

which constitutes a visual change. This interpretation could be tested by using a task design that allows to directly quantify criterion, e.g., by using a two-alternative forced choice (2AFC) task.

Note that the split over participants is orthogonal to the two splits over trials, and the fact that they produced very similar results provides some confidence in the validity of our findings. Here, we recorded a larger sample size compared to previous experiments, and we performed both fixed effects and random effects statistical testing, using for the analysis the methods that, to our knowledge, provide the best trade-off between sensitivity and specificity.[11] We stress the need in the field for studies with higher statistical power,[47] random effects statistics,[48] and a careful consideration in the choice of the analysis methods.[11,12,49]

In conclusion, when all trials were pooled, we did not find evidence for a consistent modulation of hit rate in a detection task where the probe was presented at variable times after a self-paced button press. However, we did find some indications for action-related modulation at ≈17Hz in a subset of trials and participants, which may have been characterized by lower attentional engagement or alternatively higher response criterion. These results should be taken with caution, because they were not initially hypothesized and are the result of a post-hoc splitting. However, they are suggestive of an interaction between attentional sampling dynamics and internal state, and further studies investigating this possibility may help to reconcile discrepancies between different studies in the field. Future experiments could therefore consider measuring physiological indicators of arousal, such as pupil diameter, heart rate variability, respiration rate, skin conductance, and subjective reports of absorption in the task.[50]

Limitations of the study

It is important to acknowledge the limitations of our study and clarify the scope of the results. First, this study did not allow

for a dissociation between criterion and sensitivity, which would have been possible by using a discrimination task, or a detection task with a much higher proportion of catch trials. Second, this study was not initially designed to perform the splitting procedures and the task design was not optimized for that purpose. A continuous task without any breaks between trials and blocks would have been more optimal for this purpose. Additionally, because of this, the pupillary signal was not recorded in a continuous way, which would have permitted a deconvolution of eye movement responses.

Furthermore, the lack of EEG recordings did not allow us to directly access brain oscillations that are signatures of internal states, such as alpha oscillations which are known to inversely correlate with task performance. EEG recordings would have also enabled us to confirm the alignment of neural events with the button press, providing a more direct link between the observed behavioral modulations and underlying neural processes.

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by Tommaso Tosato (tommaso.tosato.office@gmail.com).

Materials availability

This study did not generate new unique reagents.

Data and code availability

- Data reported in this paper may be shared by the lead contact upon request.
- Original code was written for the data analyses and may be shared by the lead contact upon request.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

ACKNOWLEDGMENTS

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AUTHOR CONTRIBUTIONS

T.T.: Conceptualization, Methodology, Software, Formal analysis, Investigation, Data Curation, Writing – Original Draft, Writing – Review and Editing, Visualization. G.D.: Writing – Review and Editing, Visualization. G.R.: Conceptualization, Writing – Review and Editing, Supervision, Funding acquisition. P.F.: Conceptualization, Methodology, Writing – Original Draft, Writing – Review and Editing, Supervision, Project administration, Funding acquisition.

DECLARATION OF INTERESTS

P.F. has a patent on thin-film electrodes, and he is a member of the Advisory Board of CorTec GmbH (Freiburg, Germany). The other authors declare no competing interests.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.isci.2024.111691.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Software and algorithms		
MATLAB 2021a	https://ch.mathworks.com/products/matlab.html	RRID:SCR_001622

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

We recruited participants from the general public until reaching our target sample size of 50 successful task completions (25 male, 25 female; mean age 25.6 years). Success criterion consisted of the completion of at least 300 valid trials; eight additional participants started the experiment but did not reach this minimum trial count and were therefore excluded. All participants had normal or corrected-to-normal vision and did not take any medication, except for contraceptives. The experimental protocol received approval from the ethics committee of the medical faculty at Goethe University Frankfurt (approval number 362/17). Informed consent was obtained from all participants prior to participation. Post-hoc group allocation was based on behavioral performance metrics, specifically false alarm rates, resulting in two participant groups (no false alarms: n=24; some false alarms: n=26) for subsequent analyses.

METHOD DETAILS

Apparatus

The experiment was performed in a quiet, dimly lit room. Participants sat in front of a monitor (ViewPixx, diagonal: 57.15 cm; resolution: 1920 x 1200 px; refresh rate: 120 Hz) at a distance of 65 cm, with their head stabilized by a chin rest. Stimuli were generated in Matlab using Psychtoolbox-3. Eye position and pupil size were measured with an infrared eye tracker (EyeLink 1000, SR Research). Button presses at the beginning of each trial were recorded with a response box (fORP, 4 buttons Curved-Left, Cambridge Research Systems). The relevant time stamps were recorded by the EyeLink Host PC (both the ViewPixx monitor and the fORP response box were connected to the EyeLink screw-card, which was sampled at 1000 Hz by the EyeLink Host PC). Behavioral reports at the end of each trial were recorded with a numerical keypad.

Stimuli and experimental procedure

The trial started with the presentation of a central fixation point (a 2-dimensional Gaussian of sigma = 0.5° of visual angle) on a gray background, and of two vertical fiducial lines situated around the horizontal meridian, 7.3° to the right of the fixation point. The participant was instructed to start fixating the fixation point as soon as it appeared and to keep fixating until it disappeared. Additionally, the participant was instructed to press a button on the response box, with the index finger of the right hand, in a time window ranging from 0.8 to 3.8 s after the start of the trial. The button press was followed by a probe onset interval (POI), ranging from 0.1 to 1.1 s, in which the participant had to monitor the location between the two fiducial lines for the appearance of the probe. The probe (a 2-dimensional Gaussian of sigma = 0.6°) was flashed for 8.3 ms (one frame given the monitor update frequency) between the 2 fiducial lines after the POI had elapsed. After a further variable time of 0.9 to 2.3 s, the fixation point and the fiducial lines disappeared from the screen, and the question "Have you seen the target?" appeared. The participant had to respond with the left hand pressing on a numeric keypad either the button 4 or 6, which were respectively labeled as "Yes" and "No".

The POI assumed values ranging from 0.1 to 1.1 s, with a uniform probability distribution in time. 10% of the trials did not include a probe, i.e., were "catch trials". Behavioral reports of probe detection were coded as 1 for a "Yes" response and -1 for a "No" response, and these values are referred to as behavioral response value (BRV).

Each participant performed a total of 430 trials distributed in 18 blocks of 24 trials each (~140 seconds per block). After the completion of block 9, participants were asked to take a longer break and were offered water and a little snack. In 2 participants, this break occurred later (after block 11, and after block 14), and one participant skipped the break.

For each participant, a short preparatory session with a staircase procedure was used to obtain the participant-specific contrast threshold. The contrast resulting in 50% hit rate was selected as initial value for the main task. During the main task, the probe contrast was kept constant within each block. Between blocks, the contrast was slightly adjusted to maintain 50% hit rate and compensate for possible perceptual learning or tiredness.

The trials in which the button was pressed too early (earlier than 0.8 s after the start of the trial), or too late (later than 3.8 s after the start of the trial), and the trials in which no response was given, were marked as invalid and excluded from further analysis. Additionally, trials in which the gaze of both eyes was exceeding a distance of 50 pixels (corresponding to 1.1°) from the fixation point in the 100 ms preceding the probe onset were marked as invalid.

Hit rate

The BRV average over valid non-catch trials was defined as the hit rate. We also calculated the hit rate time course (HRTC) as a function of the POI time (Figures 2 and 3). We considered the time interval between 0.1 s and 1.1 s after the button press. The BRVs were arranged accordingly to their POIs, and they were convolved with a Gaussian of sigma=0.01 s in steps of 0.001 s. All the resulting time courses were linearly detrended and averaged over participants to give one mean ATC.

Subdivision of the session into epochs

We subdivided each session into epochs characterized by higher or lower average performance. We calculated the time interval between the fixation onset of the first trial in the session and the probe onset of each trial, and called this measure ''time on task''. We analyzed task performance as a function of time in the session, by convolving the BRVs with a Hann window of 700 s length, and we referred to the obtained time course as local performance. The local-performance time course over the entire session was fit with a linear regression, to take into account a possible linear trend affecting performance along the session (e.g., decreasing performance due to increasing tiredness). Task epochs whose local performance was higher than the linear trend were labeled as ''high performance epochs''; task epochs whose local performance was lower than the linear trend were labeled as ''low performance epochs''.

Microsaccades detection

Trials during which the eye signal deviated by more than 100 pixels (approximately 2°) from the fixation point during the 200 ms prior to the target onset were marked as invalid and excluded from further analyses. The vertical and horizontal eye position signals (from 400 ms before to 1100 ms after the button press) were filtered with a low-pass Butterworth filter (2nd order with low-pass cutoff at 40 Hz). The first 100 ms were discarded to allow the filter to settle. The temporal derivatives of the filtered eye signals were taken as horizontal and vertical velocities, and they were combined to obtain overall eye speed for each eye separately.

For each participant and each eye, a specific velocity threshold was calculated. The velocity threshold was set at the median velocity plus 4 times the standard deviation of the velocity, calculated using the data from the 100 ms before the target onset. Microsaccades were detected as peaks in eye speed crossing the participant-specific threshold. Only binocular microsaccades, defined as microsaccades occurring in both eyes within a maximum temporal distance of 8 ms, were used for further analysis. Microsaccades separated by less than 60 ms from a previous microsaccade were considered detection artifacts due to post-saccadic oscillation and were removed.

For each trial, we counted only the microsaccades occurring during the period when a probe could actually appear, i.e., between 100 ms after the button press and the appearance of the probe in that trial. The microsaccade rate of a participant (during a given condition, like low-performance epochs) was defined as the cumulative sum of microsaccade counts across trials (of that condition) divided by the cumulative time (in that condition) during which these microsaccades were detected.

Pupillary response analysis

The pupillary response was analyzed to investigate potential changes in arousal and attentional states. Pupil diameter was recorded for each trial separately, using an eye tracker (EyeLink 1000, SR Research).

Preprocessing steps were applied to the pupillary trace of both eyes separately. The code checks for the presence of blinks. Blink start and end times were identified, and the blink intervals were extended by 80 ms before and after to account for partially occluded pupil data. Linear interpolation was then performed to replace the missing data during the blink intervals.

The mean pupil diameter was calculated for each trial by averaging the pupil diameter values within the temporal interval of interest, defined as the temporal interval from the button press to 100 ms after the button press. The code selects the pupil data from either the left or right eye based on the total number of valid trials for each eye. The eye with the higher number of valid trials is chosen, and the corresponding pupil diameter values are used for further analysis.

Spectral analysis

To study phase locking effects at different frequencies, we applied the single-trial least square spectral analysis (stLSSA) (Tosato et al., 2022). As a preprocessing step, we linearly detrended and tapered the BRVs of each participant. To do so, we fit a line to the participant-specific ATC and we subtracted the value of this line at the time point of each trial's POI from the respective BRV. Similarly, to taper single trials, the value of a Hann taper at the time point of each trial's POI was multiplied with the respective BRV.

We then calculated a multivariate generalized linear model separately for each participant, using as independent variables, per frequency, the probe onset phases of all trials, and as dependent variables the corresponding BRVs. The model can be written as follow:

$$\widehat{Y}_n = \beta_0 + \beta_1 \sin(2\pi f t_n) + \beta_2 \cos(2\pi f t_n)$$

Where $\widehat{Y}_n$ are the predicted BRVs, $\beta_0\ \beta_1\ \beta_2$ are the regression coefficients, f is the tested frequency, and t_n are the POIs. The regression parameters were estimated using the standard least square method as follow:

$$\widehat{B} = (X^T X)^{-1} X^T Y$$

Where:

$$Y = \begin{bmatrix} y_1 \\ y_2 \\ \vdots \\ y_n \end{bmatrix}$$

$$X = \begin{bmatrix} 1 & sin(2\pi ft_1) & \cos(2\pi ft_1) \\ 1 & sin(2\pi ft_2) & \cos(2\pi ft_2) \\ \vdots & \vdots & \vdots \\ 1 & sin(2\pi ft_n) & cos(2\pi ft_n) \end{bmatrix}$$

$$B = \begin{bmatrix} \beta_o \\ \beta_1 \\ \beta_2 \end{bmatrix}$$

The regression coefficients β_1 β_2 were then combined as the real and the imaginary part of the complex Fourier coefficient for the frequency f. We repeated this procedure for all frequencies of interest, such that we had a complex number per frequency, which can be considered as the equivalent of a complex Fourier spectrum. As frequencies of interest, we used all frequencies between 1 Hz and 40 Hz, in steps of 0.25 Hz. These calculations were done at the level of the single participant, such that each participant gave one complex spectrum. The complex spectra of all participants were then averaged in the complex domain, i.e. taking phase information into account, to obtain a single complex spectrum. This complex spectrum was rectified and squared to obtain the power spectrum.

QUANTIFICATION AND STATISTICAL ANALYSIS

Software and statistical approach

All analyses were performed using MATLAB 2021a (MathWorks). Statistical significance was set at $p < 0.05$ for all analyses.

Sample size and condition-specific counts

The total sample comprised 50 participants. Based on false alarm rates, participants were divided into two groups: those with no false alarms (N=24) and those with at least one false alarm (N=26).

Across all experimental conditions, we analyzed a total of 17,616 valid trials. The epoch-based analysis included 9,825 valid trials in low performance epochs and 7,791 trials in high performance epochs. The analysis of trial history effects included 7,502 trials following misses and 6,779 trials following hits. First trials of each experimental block were excluded from the trial history analysis due to the absence of immediately preceding trial information.

Statistical inference

In this study we performed two different levels of inference: 1) An inference on the sample of investigated participants, referred to here as fixed-effects analysis. 2) An inference on the population of all possible participants (or all possible participants fulfilling a certain selection criterion, like no false alarms), referred to here as random-effects analysis.

The fixed-effects analysis was based on a randomization at the trials level. In this case we compared our observed spectra with a distribution of bias-estimate spectra. Each bias-estimate spectrum was obtained by randomly combining POIs and BRVs at the single participant level, calculating a spectrum per participant, and averaging those spectra over participants. This randomization was performed 5000 times, and from each resulting bias-estimate spectrum, we retained the maximal values across all frequencies. If the value for a given frequency in the observed spectrum was larger than the 95th percentile of the maximal-value distribution, we considered that frequency bin significant at $p<0.05$ with multiple comparison correction across frequencies.

The random-effects analysis is based on a randomization at the participants' level, and it allows us to make an inference on the population. We performed random-effects tests (1) to test for the presence of action-related modulation compared to bias estimates, (2) to test for a difference in action-related modulations between subsets of trials or participants. For option (1), we proceeded as follows: For each participant, we had the observed spectrum and the bias-estimate spectrum (averaged over the 5000 randomizations). A paired t-test between the observed and the bias-estimate spectra, across participants, separately per frequency, gave the observed t-value spectrum. Note that the observed and the bias-estimate spectra are complex spectra, such that the t-value spectrum is also first a complex spectrum, of which we then take the absolute value. We then randomly exchanged conditions at the level of the participant. That is: To implement one randomization, we made a random decision, per participant, of whether to exchange the observed spectrum with the bias-estimate spectrum, or not. We then proceeded as before, arriving at one randomization t-value spectrum. This randomization was repeated 5000 times, and from each resulting t-value spectrum, we retained the maximal value across all frequencies. If the t-value for a given frequency in the observed spectrum was larger than the 95th percentile of the maximal-value distribution, we considered that frequency bin significant at $p<0.05$ with multiple comparison correction across frequencies.

For option (2), we proceeded identically, except that the bias-estimate spectrum was replaced by the spectrum from the other subset of trials or participants.

The testing procedures described in the last two paragraphs implement *multiple comparisons correction* across frequencies according to the max-based approach.[51] After each randomization, the maximal value across all frequencies was placed into the maximal-value distribution. Note that those distributions lack a frequency dimension. The 95th percentile of those distributions is the threshold for statistical significance with a false-positive rate of 0.05, including correction for the multiple comparisons across frequencies. Correspondingly, the observed power or t-value spectra were compared against those thresholds.

Additional measures

For pupillary response and microsaccade analyses, we used paired t-tests to compare conditions across participants (N=50). Pupil diameter values were compared between low and high performance epochs, and between trials following hits versus misses. Similarly, microsaccade rates were compared between conditions using paired t-test.