Rhythmic gain control during supramodal integration of approximate number

Bernhard Spitzer [a,*], Felix Blankenburg [a], Christopher Summerfield [b]

[a] Neurocomputation and Neuroimaging Unit, Department of Education and Psychology, Freie Universität Berlin, Habelschwerdter Allee 45, 14195 Berlin, Germany
[b] Department of Experimental Psychology, University of Oxford, Oxford OX1 3UD, UK

ABSTRACT

According to one view, neural oscillations structure information processing in time, determining whether sensory inputs have a strong or weak impact on behavior. Recent work showed that during sequential integration of visual inputs, stimuli that fall in the preferred phase of slow (1–3 Hz), endogenous EEG activity carry greater weight in subsequent judgment. Here, we asked two questions. Firstly, is this phenomenon modality-specific, or is it supramodal? Secondly, does this effect occur at the level of sequential encoding, or only during decision formation? We analyzed scalp EEG recordings from healthy human participants while they compared the approximate number of visual, auditory or somatosensory pulses in two successive intervals (N1 and N2). Despite differences in activity evoked in different domains, a common, slowly-oscillating (~3 Hz) choice-predictive signal was observed in all three modalities with a maximum coincident with pulse onset. Critically, this signal was present during N2 (when a decision was being formed) but absent during N1 (when perceptual information was encoded, but no decision could be made). In other words, rhythmic gain control during sequential processing is a supramodal phenomenon that occurs while information is integrated towards a categorical decision.

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Introduction

The electrical activity produced by the central nervous system tends to exhibit oscillatory dynamics, both at the level of local microcircuits and across large-scale cortical networks. A longstanding controversy concerns the role of neural oscillations in shaping the computations that underlie behavior. One view holds that electrical oscillations are epiphenomena of the biophysical mechanisms underlying neural circuits, and play no causal role in information processing or behavior (Shadlen and Movshon, 1999). An alternative account proposes that the phase, amplitude and frequency of neural oscillations actively encode information relevant to a current task (Buzsáki and Draguhn, 2004). One emerging theory suggests that during perception, neural oscillations might act to structure information processing across time, by periodically gating neural excitability and thereby providing temporal windows of privileged information processing and transfer (Schroeder and Lakatos, 2009; VanRullen et al., 2011). For example, in the sensory cortices of macaque monkeys, the gain of single-neuron responses is heightened when they fall in phase with oscillations entrained by rhythmic stimulation (Lakatos et al., 2007, 2008). Consistently, rhythmic entrainment of cortical oscillations was found to modulate human

observers' performance in various perceptual tasks (e.g., Cravo et al., 2013; Henry and Obleser, 2012; Ng et al., 2012; Stefanics et al., 2010).

Evidence is mounting that psychophysical performance also depends on the phase of spontaneous, endogenously ongoing brain rhythms. Visual, auditory, or tactile stimuli are more likely to be detected or discriminated when they fall in the preferred phase of ongoing cortical oscillations near the alpha-frequency range (Ai and Ro, 2014; Busch et al., 2009; Hanslmayr et al., 2013; Mathewson et al., 2009; Strauß et al., 2015). Complementing these findings, endogenous rhythmic fluctuations at a lower frequency (delta, ~1–3 Hz) were recently reported during sequential accumulation of multiple inputs over time (Wyart et al., 2012). In that study, observers integrated the information provided by successive visual events occurring in rapid sequence to make a category judgment. Those events that fell in the preferred phase of an endogenous delta oscillation were found to be more influential in determining choices, as if momentary inputs were rhythmically gated during entry to a cumulative decision variable. Low-frequency oscillatory gating of sequential information may contribute to attentional selection and temporal anticipation (Cravo et al., 2013; Stefanics et al., 2010), and may ultimately provide periodic refractory periods that guard against catastrophic interference and information overload in neural processing (Marois and Ivanoff, 2005; Sergent et al., 2005).

However, although support for this view is growing, two factors limit the conclusions that can be drawn from existing studies. Firstly, slow endogenous fluctuations in sequential processing have thus far been studied mostly in the visual domain (Wyart et al., 2012, 2015;

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but see e.g., Giraud and Poeppel, 2012 for discussion of low-frequency oscillations in speech processing). It is thus unclear whether phase-dependent gain control of to-be-accumulated sensory inputs is a ubiquitous, supramodal phenomenon, or one that depends on the modality of sensory input. Secondly, the processing stage at which gating occurs remains unclear. Signals could be gated at an early processing stage, during sequential encoding, or later, during conversion to a decision signal, and extant studies have failed to distinguish between these possibilities.

Here, we addressed these two questions directly. To do this, we capitalized on data from a previously published experiment in which human observers compared the approximate number of pulses occurring in two successive intervals (N1 and N2; see Spitzer et al., 2014). In separate conditions, pulses were administered in the visual (blinks) auditory (beeps), and somatosensory (electrical pulses) domains. Here, we used convolution modeling of scalp electroencephalographic (EEG) data to estimate how the weight (or choice-predictiveness) associated with each pulse varied over time. We observed evidence for a rhythmic, phase-dependent gain control in centro-parietal signals at ~3 Hz in all three modalities, suggestive of a supramodal phenomenon. Critically, this modulation accompanied decision formation in interval N2 but was entirely absent in interval N1, when participants accumulated the pulses in the reference interval for later comparison. In other words, endogenous, delta-rhythmic gain control during perceptual decisions occurs at a late processing stage, during conversion of perceptual signals into a decision variable.

Materials and methods

Subjects

Twenty-six healthy volunteers (22–35 years; 17 female, 9 male) gave written informed consent to participate in the experiment. Each participant received a reimbursement of 30 Euros. Two participants (1 female, 1 male) were excluded from analysis due to excessive ocular and movement artifacts in the EEG data. The study was approved by the ethics commission of the Free University Berlin and was conducted in accordance with the Human Subjects Guidelines of the Declaration of Helsinki.

Stimuli, task, and procedure

The experimental setup was described in detail in a previous paper, which focussed on working memory (delay-period) activity in the same data set (Spitzer et al., 2014). All stimuli were presented bilaterally at comfortable supra-threshold intensity levels. Visual pulses (50 ms) were delivered by white light-emitting diodes mounted to the left and the right of fixation on a TFT screen in front of the subject. Acoustic pulses were 1 kHz sine tones of 50 ms duration (including 2.5 ms fade-in/out to prevent clicking artifacts), delivered by desktop loudspeakers. On somatosensory trials, square-wave electric median nerve stimulation (200 μs) was delivered via pairs of adhesive electrodes attached to both wrists. Pulse sequences (N1/N2) were presented within 2 s integration intervals, the on- and offsets of which were signaled by a color change of the visual fixation cross (see Fig. 1A). Each pulse was randomly allocated with equal probability to one of 13 equidistant positions between 100 and 1900 ms, permitting a maximum pairwise repetition rate of 6.67 Hz. The positions of pulses/no pulses in each interval were randomly shuffled afresh on each trial in the running experiment, with no restrictions on the temporal structure of the resulting sequences. Prior to each block of trials, a visual cue ("seeing", "hearing", or "feeling") indicated the modality of the forthcoming trials. On each trial, a standard sequence (N1) was first presented (3–8 pulses, randomly varied), followed by a 3 s delay. After the delay, the comparison sequence (N2) was presented, which always contained the number of pulses in N1 ± 1 pulse, but with an independently randomized temporal structure.

Subjects were instructed to respond only after N2 interval offset (cf. color change of the fixation cross, Fig. 1A, right) by pressing a right foot pedal to indicate that N2 was larger than N1, and pressing a left pedal otherwise. Using pedal (rather than manual) responses averted upper limb movements that could have interfered with the somatosensory stimulation setup. On average, responses were given 916 ms after N2 interval offset. After each trial, full informative visual feedback was provided, by two "+" (correct) or "−" (incorrect) signs flanking the fixation cross for 200 ms. Each subject completed 6 sessions each comprising 6 blocks (2 of each modality, in counterbalanced, pseudo-random order) of 12 trials, yielding a total of 144 trials per modality. Control analysis verified that task performance levels remained stable over the course of the experiment [$F_{(5,115)} < 1$; ANOVA across task sessions].

Behavioral analysis

To estimate how participants weighted the N1- and N2-intervals into subsequent choice, we used a *psychophysical reverse correlation* technique (Neri et al., 1999; Kiani et al., 2008). Specifically, we examined for each time bin t of the two stimulation intervals the relative *excess rate* of pulses on trials subsequently judged "N2 > N1", as compared to "N2 < N1" (for a similar approach, see e.g., Raposo et al., 2012). Excess rates were computed as

$$excess\ rate_t = \frac{\sum_i u_{t,i}(\text{"N2>N1"}) - \sum_i u_{t,i}(\text{"N2<N1"})}{\sum_i u_{t,i}(\text{"N2<N1"})} \quad (1)$$

where $\sum_i u_{t,i}$ is the sum of pulse units $u_{t,i}$ over trials i. Pulse units $u_{t,i}$ were defined for any given trial i according to

$$u_{t,i} = \frac{1}{N1_i + N2_i} \quad (2)$$

for each time bin where a pulse occurred, and zeroed for each time bin where no pulse occurred. The trial-specific normalization of u with respect to overall pulse count (Eq. (2)) ensured that the excess rates reflected the influence of information in the subsequent relative comparison between the two intervals, as was demanded in the behavioral task, rather than judgment of each interval in isolation. In the absence of response bias, the excess rate at time bin t is expected to be zero if choices were uncorrelated with the physical input at that time (i.e., if the objective information at time t had been ignored in the subjective N2-N1 comparison). To the extent that choices were correlated with the input at time t (i.e., the information had *weight* in the decision), the excess rate will differ from zero. In our two-interval task, excess rates according to (1) will reflect decision weighting within the N2- and N1 intervals with opposite signs (since stronger weighting of N2 pulses favors "N2 > N1"-choices, whereas stronger weighting of N1 pulses favors the opposite choice). Thus, for comparative analysis and interpretation (Figs. 1B-C), we infer decision weighting (w) of the N2-interval from excess rates directly [Eq. (3); Figs. 1B/C, *right*], and the weighting of the N1-interval from excess rates with a flipped sign [Eq. (4); Figs. 1B/C, *left*].

$$w_{t(N2)} = excess\ rate_{t(N2)} \quad (3)$$

$$w_{t(N1)} = -excess\ rate_{t(N1)} \quad (4)$$

EEG recording and analysis

EEG was recorded from 64 active electrodes (BioSemi ActiveTwo, Amsterdam, Netherlands) configured according to the extended 10–20 system. Ocular activity was registered via two pairs of additional electrodes placed in standard bipolar montages (vertical and horizontal)