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Duration estimation entails predicting *when*

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ABSTRACT

The estimation of duration can be affected by context and surprise. Using MagnetoEncephaloGraphy (MEG), we tested whether increased neural activity during surprise and following neural suppression in two different contexts supported subjective time dilation (Eagleman and Pariyadath, 2009; Pariyadath and Eagleman, 2012). Sequences of three 300 ms frequency-modulated (FM, control) or pure tones (test) were presented and followed by a fourth FM varying in duration. In test, the last FM was perceived as significantly longer than veridical duration (Tse et al., 2004) but did not differ from the perceived duration in control. Several novel and distinct neural signatures were observed in duration estimation: first, neural suppression of standard stimuli was observed for the onset but not for the offset auditory evoked responses. Second, ramping activity increased with veridical duration in control whereas at the same latency in test, the amplitude of the midlatency response increased with the distance of deviant durations. Third, in both conditions, the amplitude of the offset auditory evoked responses accounted well for participants' performance: the longer the perceived duration, the larger the offset response. Fourth, neural duration demarcated by the peak latencies of the onset and ramping evoked activities indexed a systematic time compression that reliably predicted subjective time perception. Our findings suggest that interval timing undergoes time compression by capitalizing on the predicted offset of an auditory event.

Introduction

Whether time perception results from a specialized centralized clock in the brain, emerges from the dynamics of state-dependent neural networks or a combination of both has challenged time research over the years (e.g. for reviews, Buhusi and Meck, 2005; Eagleman et al., 2005; Karmarkar and Buonomano, 2007; Tucci et al., 2014; van Wassenhove, 2009; Wittmann and van Wassenhove, 2009). One approach to understand perception at large is to characterize when the brain fails to represent the world in a veridical manner; in time research, one can capitalize on temporal illusions in which the perceived duration of an event differs from its veridical duration. Temporal illusions and subjective distortions of duration have been reported within and across sensorimotor modalities under various experimental conditions (Ayhan et al., 2009; Bruno et al., 2010, 2013; Henry and McAuley, 2013; Herbst et al., 2012; Johnston et al., 2006; Kanai et al., 2006; Morrone et al., 2005; New and Scholl, 2009; Pariyadath and Eagleman, 2007; Rose and Summers, 1995; Ulrich et al., 2004; van Wassenhove et al., 2011; Wittmann et al., 2010; Yarrow et al., 2001). For instance, surprising and unexpected events are often reported to last subjectively longer than they really are (Eagleman and Pariyadath, 2009; Kim and McAuley, 2013; Pariyadath and Eagleman, 2007; Rose and Summers, 1995; Tse et al., 2004; van Wassenhove et al., 2008). One possibility is that attention allocated to a surprising or unpredictable event underlies the subjective dilation of time (Tse et al., 2004; Ulrich et al., 2004) by increasing the rate of the internal clock in agreement with the fundamental role of attention in clock models (Meck, 1984). Alternatively, hypotheses based on coding efficiency suggest that standard events during neural repetition suppression could undergo temporal compression (Eagleman and Pariyadath, 2009; Pariyadath and Eagleman, 2012): hence, subjective temporal dilation could result from the temporal compression of predictable events (the standard stimuli in a sequence), from an increased neural response elicited by surprise (the oddball event in a sequence of standard events) or a combination of both. In both views, one major question is to which extent the context in which an event is presented affects its perceived duration and its associated neural response.

To experimentally address this question, we designed an auditory oddball paradigm in which the stimuli whose duration had to be estimated were all physically identical but presented in two different contexts or sequences of standard events. We specifically asked whether the auditory evoked responses elicited by an auditory oddball – the last stimulus in the sequence – differed as a function of context. The typical response to oddball stimuli is the MisMatch Negativity (MMN) – and its magnetic equivalent, the MisMatch Field (MMF) – which is elicited by the presentation of a surprising event in the context of a repeated stimulation. MMN/Fs naturally entail neural suppression and are classically considered an index of automatic change detection (Näätänen, 1995). While the functional role of neural suppression is

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debated (Gotts et al., 2012; Grill-Spector, 2006), the Bayesian "explaining away" (Gotts et al., 2012) suggests that repetition of the same information refines an internal template subsequently used to generate an hypothesis as to the impending sensory evidence. The MMN/Fs is thus an index of predictive coding (Friston, 2005; Garrido et al., 2009; Kiebel et al., 2008; Wacongne et al., 2012) sensitive to the depth of complexity in the internal model that has been generated on the basis of the statistics of the inputs (Wacongne et al., 2011). Whether duration is one of the possible properties that can be predicted by a generative internal model is unknown.

The elicitation of MMN/F by duration oddballs reported in human adults (Joutsiniemi et al., 1998; Kaukoranta et al., 1989; Näätänen et al., 1989; Tervaniemi et al., 1999), children (Kushnerenko et al., 2001) and rats (Roger et al., 2009) suggests that temporal information can be automatically encoded and thus, that an internal template for duration is possible. In a seminal report, the existence of an MMN elicited by duration changes was taken as supporting evidence for a memory trace and for the possible existence of duration neurons in auditory cortex (Näätänen et al., 1989). In early studies, the MMN elicited by tones longer than standards were larger than those elicited by tones of shorter duration (Catts et al., 1995; Jaramillo et al., 1999; Näätänen, 1992; Näätänen et al., 1989); the reverse has also been reported, namely: MMN elicited by shorter durations can be larger than those elicited by longer durations (Colin et al., 2009). Importantly, the amplitude of the MMN has also been reported to correlate with perceptual accuracy of duration estimates (Amenedo and Escera, 2000) and consistent with the MMN as an index of residual error in predictive coding, the more distant the deviant duration was from the standard (irrespective of being shorter or longer), the larger the recorded MMN (Jaramillo et al., 2000). One important issue is that MMN/F obtained to the presentation of duration oddballs have typically been generated by stimuli that were physically different: as such, the MMN/F could have provided erroneous estimations of duration deviance if standard and oddball stimuli underwent different neural analysis (Jacobsen and Schröger, 2003).

Our experimental design addresses this specific concern by contrasting identical duration auditory oddballs in two different contexts (Fig. 1):

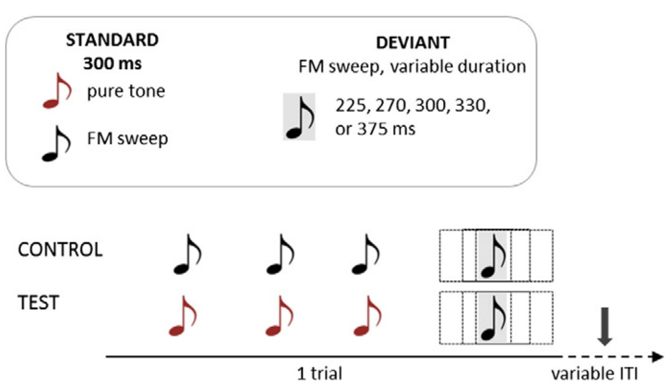

Fig. 1. Experimental paradigm. The experimental design was blocked with TEST and CONTROL trials ran separately. The order of presentation was counter-balanced across participants. One experimental trial consisted of four consecutive auditory stimuli: three standard sounds (STD) followed by one deviant sound (DEV). In CONTROL, all four standards were ascending FM sweeps (from 850 Hz to 1050 Hz); in TEST, the first three stimuli were pure tones (centered on the FM sweep, 950 Hz) and the fourth stimulus was an upward FM sweep (going from 850 to 1050 Hz). In both CONTROL and TEST, the first three STD lasted 300 ms whereas the fourth stimulus (DEV) lasted one of five possible durations as follows: 300 ms, 300 ± 30 ms (10% of the STD duration), or 300 ± 75 ms (25% of the STD duration). DEVs were always upward FM sweeps whose duration varied. Hence, the identity of the STD sequence determined whether the deviance was solely based on duration (CONTROL) or on duration and feature space (TEST). Inter-stimulus-intervals (ISIs) were pseudo-randomly chosen from 350 ms to 650 ms; inter-stimulus intervals (ITIs) were pseudo-randomly chosen from 666 ms to 1000 ms following participants' response. Participants were asked to report whether the duration of the last stimulus was longer or shorter than the first three stimuli in the preceding sequence.

in CONTROL or predictable condition, the oddball stimuli were identical to the standard stimuli with a parametric change in duration; in TEST or surprising condition, both the identity and the duration of the oddball stimuli were varied. The prediction was that the duration in TEST would elicit subjective temporal dilation as compared to veridical time and CONTROL; we report significant subjective temporal dilation in TEST as compared to veridical duration but not as compared to CONTROL. In both contexts, we expected the presence of an MMF at the offset response of the oddball stimuli which would display a residual error profile as a function of duration. However, we report a more intricate pattern of results: in CONTROL, a clear ramping activity starting at the onset response and peaking prior to the auditory offset (or duration MMF) response could be observed; similarly in TEST, a midlatency evoked response preceding the auditory offset (or duration MMF) response was observed. While the peak of midlatency ramping activity showed a linear increase with veridical duration in CONTROL, a residual error pattern at the same latency was observed in TEST. In both TEST and CONTROL, the offset response or duration MMF showed a linear increase with veridical duration. Finally, quantifying the "neural duration" between the most reliable and consistently recorded onset response (namely, the auditory m100) and the peak of midlatency ramping activity provided a good approximation of perceived timing albeit predictably compressed by 40 ms.

Material and methods

Participants

Fifteen healthy participants took part in the study. None had any known neurological or psychiatric disorder and all had normal hearing. Three participants were taken out of the study due to low SNR (signal-to-noise ratio) and contamination by eye artifacts of the MEG data, leaving 12 participants (mean age of 24.3 years old, 5 females). Written informed consents were obtained from each participant in accordance with the Declaration of Helsinki (2008) and the Ethics Committee on Human Research at the Commissariat à l'Energie Atomique et aux Energies Alternatives (CEA/DSV/I^{2}BM/NeuroSpin, Gif-sur-Yvette, France). All participants were compensated for their participation.

Stimuli

The experimental paradigm (Fig. 1) was designed using Psychtoolbox (Brainard, 1997) with Matlab v2009b (Mathworks Inc.). A white fixation cross was constantly presented on a black screen to help participants maintain eye fixation. Each trial consisted of a sequence of four binaural auditory stimuli. The first three stimuli in the sequence were standards of 300 ms duration (STD1, STD2, STD3). In the control condition, the standards were upward frequency-modulated (FM) sweeps spanning 850 Hz to 1050 Hz over the 300 ms; in the test condition, the standards were sinewave tones (950 Hz). In both control and test, the fourth stimulus in the sequence was a deviant (DEV) which consisted of an FM sweep spanning 850 Hz to 1050 Hz with variable duration. The deviant could last 300 ms (DEV3), ±10% of the standard duration (DEV2: 270 ms or DEV4: 330 ms) or ±25% of the standard duration (DEV1: 225 ms or DEV5: 375 ms). Hence, in the control condition, STD and DEV were identical in feature space (FM sweeps) and the deviant solely differed from the STD in duration; in the test condition, STD and DEV differed both in feature space (tone vs. FM sweep) and in duration. All sounds had a 5 ms ramp on/off.

Inter-Stimulus Intervals (ISI) were pseudo-randomly selected from a 350 to 650 ms. A variable ISI was used to prevent participants to use a rhythmic cue to perform the task. Additionally, Inter-Trial Intervals (ITIs) were pseudo-randomly selected from 666 to 1000 ms and started after participants had entered their response.

The task consisted in judging whether the last stimulus – i.e. DEV – in the sequence was shorter or longer than all other preceding