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Small perturbations in a finger-tapping task reveal inherent nonlinearities of the underlying error correction mechanism

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ABSTRACT

Time processing in the few hundred milliseconds range is involved in the human skill of sensorimotor synchronization, like playing music in an ensemble or finger tapping to an external beat. In finger tapping, a mechanistic explanation in biologically plausible terms of how the brain achieves synchronization is still missing despite considerable research. In this work we show that nonlinear effects are important for the recovery of synchronization following a perturbation (a step change in stimulus period), even for perturbation magnitudes smaller than 10% of the period, which is well below the amount of perturbation needed to evoke other nonlinear effects like saturation. We build a nonlinear mathematical model for the error correction mechanism and test its predictions, and further propose a framework that allows us to unify the description of the three common types of perturbations. While previous authors have used two different model mechanisms for fitting different perturbation types, or have fitted different parameter value sets for different perturbation magnitudes, we propose the first unified description of the behavior following all perturbation types and magnitudes as the dynamical response of a compound model with fixed terms and a single set of parameter values.

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1. Introduction

Time perception and production in the range of several hundreds of milliseconds, known as millisecond timing, is crucial for motor control, speech generation and recognition, playing music and dancing, and rapid sequencing of cognitive operations such as updating working memory (Buhusi & Meck, 2005; Meck, 2005). However, our understanding of the basic mechanisms underlying these behaviors is poor, and the representation of temporal information in the brain remains one of the most elusive concepts in neurobiology (Ivry & Spencer, 2004), particularly in this timing range. To date no strong consensus has been reached about which brain regions are involved in time measurement of short intervals and how they interact (Beudel, Renken, Leenders, & de Jong, 2009; Del Olmo, Cheeran, Koch, & Rothwell, 2008; Lewis & Miall, 2003; Manto & Bastian, 2007), or which is the neural mechanism responsible for the production of timed responses in this range (Buonomano & Laje, 2010). This stands in stark contrast to our rather comprehensive knowledge about temporal processing in other ranges, for example circadian timing (Panda, Hogenesch, & Kay, 2002).

1.1. Sensorimotor synchronization

A paradigmatic aspect of millisecond timing is sensorimotor synchronization, which is the ability to entrain movement to an external metronome. Although a recent study reported this ability in a variety of non-human species (Schachner, Brady, Pepperberg, & Hauser, 2009), animals display a very limited form of the behavior. In contrast, it is quite easy for humans to achieve synchronization with a metronome or musical beat and this forms the basis of all music and dance. One of the simplest tasks to study sensorimotor synchronization is finger tapping. In this task a subject is instructed to tap in synchrony with a periodic sequence of brief tones, and the time difference between each response and its corresponding stimulus is recorded (see Fig. 1). Despite its simplicity, this task helps to unveil interesting features of the underlying neural system and the error correction mechanism responsible for synchronization.

The first evidence of the existence of such a correction mechanism is the phenomenon of synchronization itself; although no single response is perfectly aligned in time with the corresponding stimulus, the responses stay in the vicinity of the corresponding stimuli throughout (see Fig. 1; note the commonly observed tendency of anticipation, called Negative Mean Asynchrony or NMA). Without a correction mechanism, tiny synchronization errors or small differences between the interstimulus interval and the interresponse interval would rapidly accumulate and make the responses drift away from the stimuli, as it is very unlikely that the subject could set his/her interresponse interval exactly at the right value—even on average. This is most evident when the subject is instructed to keep tapping at the same pace after the metronome has been muted, what is called a continuation paradigm. The "virtual asynchronies" computed between the continuing taps and the extrapolated silent beats usually get quite large within a few taps (Repp, 2005), even for musically trained subjects. Note that this crude evidence for a correction mechanism does not indicate the kind of mechanism used, since average synchronization could be achieved through either continuous adjustments (i.e., at every step), or intermittent control (i.e., once every few steps), or some other correction strategy (Gross et al., 2002), or even a mix of short- and long-range processes (Wagenmakers, Farrell, & Ratcliff, 2004).

1.2. Models for finger tapping

The behavior of the neural mechanisms underlying finger tapping synchronization is usually interpreted in terms of an error-correction function *f* that takes past events as inputs (including asynchronies, intervals, and interval differences) and estimates the timing of the next response. This approach assumes that the underlying mechanism can be separated into a deterministic part (the correction function itself) and noise (due to inherent variability of time estimation, motor action, etc., see the seminal paper on clock and motor variance by Wing & Kristofferson (1973)). The form of the error correction function can then be generally stated as:

$$e_{n+1} = f(e_n, t_n, r_n, T_n, \ldots) + \text{noise} \tag{1}$$