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Interval Timing Behavior: Comparative and Integrative Approaches Introduction to the Special

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The ability of animals to keep track of, remember, and act upon short time intervals has received growing scientific attention attested by the increasing number of papers published and scientific activities organized in this area of research. Arguably, one of the driving forces behind this dynamic is the fact that interval timing captures a fundamental currency, constituent of many derived quantities of critical biological significance. Thus, temporal information processing presumably interacts with many other processes that support the adaptiveness of organisms in their environment by operating on variables that are derived from time intervals.

A substantial number of theoretical and empirical studies indeed emphasize the relevance of interval timing for many crucial functions such as learning (Balsam & Gallistel, 2009; Gallistel & Gibbon, 2000; Savastano & Miller, 1998), decision-making (Balci, Freestone, Simen, deSouza, Cohen, & Holmes, 2011; Namboodiri, Mihalas, Marton, & Hussain Shuler, 2013), foraging (Bateson, 2003; Kacelnik & Brunner, 2002), and communication (MacDonald & Meck, 2005; Shannon, Zeng, Kamath, Wygonski, & Ekelid, 1995). Consequently, a complete understanding of many cognitive and behavioral processes and their dynamics entails the consideration of temporal information processing as an underlying process. When the adaptive value of interval timing in and of itself is coupled with its functional interaction with other adaptive functions within the framework of an evolutionary approach to cognition, it is not surprising that interval timing ability is observed in many species of animals (possibly as a primitive element of cognition) with specific psychophysical signatures (Gallistel, 1990; Buhusi & Meck, 2005).

Another driving force behind the growing interest in interval timing stems from the fact that psychological time does not rely on a sensory system that is specialized for transducing time-specific exogenous signals. The sense of time rather relies on endogenous signals and/or emerges as a by-product of neural information processing related to other functions. Importantly, the generality of timing “laws” across species (at least in vertebrates) points at the existence of common, evolutionarily preserved, and well-regulated genetic loci and neural mechanisms for the time keeping ability. To this end, a substantial number of electrophysiological and neuroimaging studies have aimed to elucidate the functional architecture and the processing dynamics of the biological stopwatch (Finnerty, Shadlen, Jazayeri, Nobre, & Buonomano, 2015; Merchant, Harrington, & Meck, 2013). Although several brain areas are implicated to be more central to interval timing (e.g., striatum, cerebellum), time-dependent neural activity is observed in many parts of the brain (e.g., thalamus, cortical areas)

suggesting the involvement of large and various networks (Merchant et al., 2013). Furthermore, electrophysiological studies revealed multiple forms of timing-related neural activity that include ramping, time-tuned responses, and oscillations (Hass & Durstewitz, 2014). The investigation of the neural basis of interval timing also relates to the question of how *representations* of simple but abstract quantities can emerge from neural information processing.

Last but not least, the clinical relevance of timing behavior is another reason behind the growing interest in this function (Allman & Meck, 2012; Balci, Meck, Moore, & Brunner, 2009b). Interval timing ability is disrupted in systematic ways in various central nervous system disorders that range from Parkinson's disease (Malapani, Rakitin, Levy, Meck, Deweer, Dubois, & Gibbon, 1998; Parker, Lamichhane, Caetano & Narayanan, 2013) to Huntington's disease (Rao, Marder, Uddin, & Rakitin, 2014), from schizophrenia (Ciullu, Spalletta, Caltagirone, Jorge, & Piras, 2015; Penney, Meck, Roberts, Gibbon, & Erlenmeyer-Kimling, 2005) to autism (Allman, DeLeon, & Wearden, 2011). Sometimes this takes the form of a disruption in temporal accuracy whereas at other times reduction in temporal precision. When these clinical findings are combined with the between-species commonalities that relate to this function, it characterizes interval timing as a promising translational model system for the preclinical animal studies (Balci, Day, Rooney, & Brunner, 2009a). Findings gathered from these studies in turn provide valuable information regarding the neurobiological basis of the time keeping ability.

We are currently at a stage where substantial amount of empirical knowledge on interval timing has been collected providing fruitful grounds for the empirical and theoretical integration of interval timing with other functions within a comparative framework. This special issue aims to contribute to this comparative and integrative approach to interval timing. The issue contains 12 research papers and one review paper presenting research by leading researchers. The readers will find that these papers address a variety of research topics that contribute to our understanding of interval timing from different angles and across species (bees, mice, rats, pigeons, humans), and of the role of this function in other cognitive domains. I will very briefly highlight the content of each paper in the rest of this Editorial.

The relationship between interval timing and circadian rhythm constitutes an interesting research topic considering the fact that both systems capture the same dimension but at different scales and with different operational characteristics and neural substrates. To this end, Bussi, Levin, Golombek and Agostino (2015; [this volume](#)) investigated the mechanisms that mediate the relationship between interval timing and circadian rhythms and showed that the circadian modulation of interval timing is mediated by the melatonin-dependent regulation of striatal dopaminergic function in the pinealectomized rats. Crystal (2015; [this volume](#)), instead, investigated the timing of hours-long inter-meal intervals (i.e., 7-13 hr), and showed that rats can also time these long intervals. The findings of these studies are informative in formulating the relationship between the different timing mechanisms of the brain.

There is also a growing literature on time-based decision-making. A number of these studies investigate the factors that affect temporal decisions and evaluate these effects in the context of decision-making and reward maximization-based models. There

are various advantages to these analytical approaches. For instance, computational models can be used to characterize the behavioral effects at the level of latent generative processes/variables (e.g., decision thresholds, temporal integration) and/or to evaluate them with respect to ecologically relevant utility functions. These models also constitute promising and rich analytical interfaces for between-species comparisons as well as the elucidation of the mapping between the behavior and the brain (Carandini & Churchland, 2013; Mulder, van Maanen, & Forstmann, 2014). To this end, Daniels, Fox, Kyonka and Sanabria (2015; [this volume](#)) investigated the effect of reward magnitude on temporal decision-making performance in pigeons, rats, and humans. Their results showed the effect of reward magnitude manipulations on response thresholds that determined the timing of switching behavior (between temporal options) in a temporal discrimination task. The direction of these effects was similar for pigeons and rats. Using a variant of the same paradigm, Çoşkun, Berkay, Sayalı and Balcı (2015; [this volume](#)) investigated the effect of probabilistic manipulations on sequential temporal discrimination between multiple options (i.e., two subsequent decisions in a trial) in mice and humans. They showed that the probabilities were adaptively integrated into the initial temporal decisions of both species. Although mice took into account the probabilistic information also for their subsequent decisions in an adaptive fashion, this was not the case for humans. These experiments extended the scope of temporal decision-making studies.

In a similar line, two studies investigated questions that had more direct implications for the models of interval timing and associative learning. To this end, Carvalho, Machado and Vasconcelos (2015; [this volume](#)) showed that the temporal context matters for the parameterization of temporal control exerted on behavior in pigeons, and evaluated their findings within the framework of an extension of the Learning to Time Model, a behavioral model of interval timing with features of associative learning. Delamater and Nicolas (2015; [this volume](#)) demonstrated that rats average the temporal relationships marked by different stimuli and learned separately, when these stimuli are presented simultaneously (stimulus compound test), under certain circumstances, and even when different stimuli predicted different discriminable rewards. These findings extended the scope of earlier findings on temporal averaging (Matell & Kurti, 2014) and are discussed in terms of how stimulus compounds influence learned behaviors (e.g., averaging vs. associative summation).

The role of dopamine in interval timing is one of the widely studied and discussed topics in the field. Castillo, Taylor, Ward, Paz-Trejo, Arroyo-Araujo, Galicia Castillo and Balsam (2015; [this volume](#)) investigated the effect of the dopaminergic manipulations (d-amphetamine and haloperidol) on the acquisition of temporal control in the rat using the peak interval procedure and tested the effect of acute withdrawal from the drug on timing behavior. They found that the encoding of time intervals was not affected by the dopaminergic manipulations; however the timing of response initiation was sensitive to the effect of these manipulations differentially during acquisition and testing depending on the drug tested.

Interval timing ability can also be used for the behavioral validation of the animal models of certain disorders that are characterized by timing deficits. The study by Brunner, Balcı, Curtin, Farrar, Oakeshott, Sutphen, Berger and Howland (2015; [this volume](#)) represents this approach in relation to Huntington's Disease (HD), which has

been previously shown to be associated with timing deficits in the clinic (Rao et al., 2014). They tested the interval timing performance of two different genetic mouse models of HD (zQ175 knockin mice and BAC HD transgenic mice) in the peak interval procedure. Their findings showed temporal control deficits in zQ175 KI but not BAC HD mice. The deficits observed in the former model are consistent with their earlier findings with R6/2 Tg (Balci et al. 2009b), a widely used transgenic mouse model of HD and indicate that both response rate and response cessation are particularly affected by the models' HD-like pathology.

The effect of sensory properties on interval timing has been studied in human studies (Matthews & Meck, 2014) but has not been investigated to the same degree in non-human animals. This empirical gap is filled by Bertolus, Knippenberg, Verschueren, Le Blanc, Brown, Mouly and Doyere (2015; [this volume](#)), who showed the important and interesting effects of sensory properties (i.e., tone frequencies) on temporal control expressed in the form of conditioned suppression of lever pressing in the cued fear conditioning as well as temporal discrimination in the rats.

Studies included in this special issue were not limited to non-human animals. In one of the human studies, Labliuk, Guilhardi, Cravo, Church and Caetano (2015; [this volume](#)) investigated the conditions that lead to stimulus control in temporal discrimination. Their findings showed that keeping the amount of training constant, the order of training with different intervals affected the emergence of the stimulus control over timed behavior (stimulus control became less likely with longer training blocks per interval). This paper points at similarities between humans and rats in terms of the conditions under which they acquire stimulus control over timing behavior. In the second human study, Grondin, Laflamme, Bienvenue, Labonté and Roy (2015; [this volume](#)) investigated how sex modulates the effect that emotional stimuli (angry and ashamed faces) have on time perception. They showed differences between the duration judgments for angry and shameful faces and interesting dependencies of these effects on sex and *empathy* (with *shame* being a secondary socially relevant emotion).

There is a limited number of studies that investigated interval timing in invertebrate species (but see Boisvert and Sherry, 2006). The primary reasons behind this gap are the difficulties in testing behaviors of invertebrates partially due to their relatively limited behavioral repertoire and the lack of effective testing protocols. With great effort I have personally made a number of failed attempts at investigating temporal control over behavior in marine crabs, and can therefore attest its difficulty. Craig & Abramson (2015; [this volume](#)) tested honeybees in the fixed-interval schedules and analyzed the data at individual subject level and after aggregating the data. Their results showed that, even if pooled group analyses point at the presence of temporal control, the analysis of individual animals negates it. This study emphasizes the importance of individual subject level analyses in the investigation of behavioral data in general, and timing behavior in particular, and present novel analytical techniques.

Finally, the review paper by Marshall and Kirkpatrick (2015; [this volume](#)) emphasizes the ubiquity of interval timing in the context of studies of cognition by presenting a comprehensive discussion of the interaction between interval timing and other functions. To this end, they outlined the role of temporal information processing in

domains such as value-based decision-making, regulation of goal directed behavior, and associative learning.

These studies made a very nice collection of papers that reflect the integrative and comparative approach to the study of interval timing. I would like to thank each and every author, who has contributed their work to this special issue, and to the editorial team which on a *pro bono* basis dedicated time and effort to this publication.

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