Evolution of temporal interaction:

A comparative approach to social timing

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Abstract: Increasing empirical research shows a deep connection between timing processes and neural processing of social information. An integrative theoretical framework for prospective studies in humans was recently proposed, linking timing to sociality. A similar framework guiding research in non-human animals is desirable, ideally encompassing as many taxonomic groups and sensory modalities as possible in order to embrace the diversity of social and timing behaviour across species. Here we expand on a previous theoretical account, introducing this debate to animal behaviour. We suggest adopting an evolutionary perspective on social timing in animals: i.e. a comparative approach to probe the link between temporal and social behaviour across a broad range of animal species. This approach should advance our understanding of animal social timing that is, how social behaviour and timing are mutually affected, and possibly of its evolutionary history in our own lineage. We conclude by identifying outstanding questions and testable hypotheses in animal social timing.

Keywords: social cognition; evolutionary neuroscience; basal ganglia; striatal beat frequency model; comparative cognition; timing; time perception.

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In the last decades, two fields of human behavioural neuroscience have grown tremendously. These are social cognitive neuroscience and the study of timing and time perception. Temporal processing and social neuroscience are becoming more and more intertwined in human research. For example, a recent review put forward a 'Socio-Temporal Brain' hypothesis predicting that an individual's temporal signature can modulate the outcome of an interaction (Schirmer, Meck, & Penney, 2016). Likewise "non-temporal social information can influence time perception and behavioral timing" (pp.10). For instance, the duration of human facial expressions affects their socio-emotional meaning, and close interpersonal relations predict enhanced movement synchrony (Schirmer et al., 2016). Contributions as these are crucial to understand basic mechanisms which link fine-grained neural processes to social behaviour. In particular, an expanded framework on social timing should help to partially refocus a field of study and get closer to basic mechanisms, by either pruning some less relevant variables or adding previously neglected factors which may influence a particular behaviour. For instance, in the particular case of human timing, decades of research have mostly focused on testing individuals in meticulously controlled environments. In contrast, we now know that an interactive social environment may be a determinant of individual timing behaviour.

In their intriguing Socio-Temporal Brain hypothesis, Schirmer and colleagues (2016) critically acknowledge the existence of (i) a bi-directional interaction between group and individual timing and (ii) cases of temporal coordination in animals. Consequently, they formulate a number of outstanding critical questions. For instance: "What brain mechanisms link social and temporal computations?", "Can we explain why socio-temporal processes appear to be lateralized to the right hemisphere?", or "Can we develop a theoretical framework that systematizes and explains the close relationship between timing and social expression and perception?" (Schirmer et al., 2006, pp.10). None of these outstanding questions refers directly to non-human animals in the original paper, though we believe they could. Here we propose a venue to answer some of these questions by further developing an integrative 'Socio-Temporal Ganglion' hypothesis across animal species. We suggest substituting the word and concept of 'brain' with that of 'ganglion', an assemblage of neurons responsible of centrally-modulated behaviour. This terminological generalization is necessary, because ganglia can be virtually found in all animal species, while brains are just found in vertebrates. Advocating a comparative and evolutionary approach, the study of a broad range of animal species has the potential to unveil both the current diversity and the evolutionary history of the socio-temporal 'brain'. We propose to pragmatically compare both behavioural and neural patterns of socially-modulated timing within and across species (Kotz & Schwartze, 2016). One reason to study within-species and between-species variability is that this approach can provide information about the evolution of a trait. If a great deal of between-individual variability is present within a species, this will suggest that natural selection can act on the trait of socially-modulated timing. For example, if some individuals have particularly developed social timing skills, and those same individuals show higher than average reproductive output, then socially-modulated timing may be an adaptive behaviour favoured through sexual selection.

Efforts in this direction are attested in animal behaviour. For instance, fiddler crabs (genus *Uca*) wave their claws in social (mostly reproductive) contexts and show complex forms of timing in these claw-waving displays (Backwell, Jennions, Passmore, & Christy, 1998; Kahn, Holman, & Backwell, 2014). Complementarily, non-temporal social information influences timing patterns of waving displays in this genus of Crustacea by modulating the temporal frequency of waving depending on the audience (Pope, 2000). Joining these parallel strands, as Pope (2000) and other colleagues have done, an integrative framework to relate timing and sociality across species is needed. This comparison could be performed by mathematically representing and quantifying timing dimensions. All this sketches an approach to answer the question: *Why* and *how* do animals show socially-modulated timing behaviour?

The comparative approach (comparing species' behaviour and cognition) is particularly insightful for understanding the evolutionary history of a trait (Fitch, Huber, & Bugnyar, 2010). In the case of the Socio-Temporal Ganglion hypothesis, comparative data are needed from species with (a) different degrees of sociality and (b) capacities for perceiving/producing complex temporal patterns. Social interaction is indispensable to trigger synchronous sound production in many species of insects, frogs, and crustaceans (e.g. Ravignani, Bowling, & Fitch, 2014; Ravignani & Cook, 2016) and can boost timing accuracy in chimpanzees synchronizing their movements to sound (Yu & Tomonaga, 2015). These behaviours echo the Socio-Temporal Brain hypothesis proposed for humans (Schirmer et al., 2016). By evolutionary homology and analogy (Fitch et al., 2010; Naumann et al., 2015), one can draw inferences on (i) the evolutionary history of social timing and (ii) the functions and mechanisms of different social timing behaviours. For instance, a number of phylogenetic factors seem to shape animal timing alone. Call duration in cetaceans mirrors - to some extent - phylogeny, with within-genus similarities and between-genus variability (Matthews, Rendell, Gordon, & Macdonald, 1999). Likewise, in different species of Túngara frogs, females are equally attracted by conspecific calls and calls of their recent ancestor, also based on temporal parameters (Ryan & Rand, 1999). Conversely, highly social synchronous chorusing is found across many taxonomic groups and sensory modalities (Greenfield & Roizen, 1993; Kahn et al., 2014; Sismondo, 1990). Synchrony often results from individuals jamming conspecifics' signals, suggesting some might be cases of convergent evolution. While these homologies and analogies are suggestive of phylogenetic and evolutionary factors in shaping one species' timing, the link between timing and sociality remains little explored in a comparative fashion.

Humans display many forms of 'social temporality' e.g. turn-taking (fine-tuned alternation) in speech compared to synchrony (events happening at the same time) in music. However, human researchers should acknowledge that many non-human species show similar behaviours. These common behaviours can be due to common ancestry or convergent evolution. For instance, plain-tailed wrens exhibit both synchronous and turn-taking behaviours in social contexts (Mann, Dingess, & Slater, 2006). This neotropical bird species performs well-timed choruses, where same-sex individuals sing similar parts in perfect synchrony, while groups of males and females alternate their complementary songs with remarkably accurate timing - latency in turn-taking can drop as low as 17 msec (Mann et al., 2006). We propose that the function of a particular timing mode in one species (e.g., wrens and gibbons singing in antiphonal alternation) may provide information on the evolutionary function of timing in other species (antiphonal timing in human speech turn-taking) (Fitch et al., 2010; Ravignani et al., 2014; Ravignani & Cook, 2016). Likewise, the body of work dealing with human social timing can serve to develop predictions and hypotheses that are testable in different taxonomic groups. For instance, timing skills of different species of *Uca* crabs or *Thryothorus* wrens can be systematically compared within a genus, and the outcome can be related to their differences in social organization.

Neurobiologically, the Socio-Temporal Brain hypothesis is built on the striatal beat frequency (SBF) model (Gu, van Rijn, & Meck, 2015; Schirmer et al., 2016). Briefly, the SBF is a neurobiological model of timing, proposing that the striatum coordinates and integrates cortical oscillations in the human brain to represent time. The SBF model hence relies on assuming strong connections between the striatum and cortex. To test both the model and the hypothesis, it would be enriching to compare timing abilities across species with varying degrees of cortico-striatal connectivity, sociality, and phylogenetic relatedness. Comparative research can develop along several directions.

First, non-human primates can be promising model species to study the neurogenetics of cortico-striatal connectivity due to existing and available data from comparative vocal perception/production studies (Enard, 2011; Rilling, 2014). In fact, at least in some primates, there is evidence for a two-way connection between the basal ganglia and cerebellum (Bostan, Dum, & Strick, 2010; Hoshi, Jean, Carras, & Strick, 2005). These two structures, evolutionarily old in vertebrate evolution, were previously thought to be quite separate and able to communicate only via more recent cortical structures. Finding two-way connections between basal ganglia and cerebellum, possibly bypassing the cortex, means that social timing might rely on evolutionary old neural structures and hence be applicable to a broad range of species.

Second, to test whether the SBF model is a necessary prerequisite for the Socio-Temporal Ganglion hypothesis, social birds could be tested (Fitch et al., 2010): As avian species lack a cortex, highly developed timing skills in social birds might point towards alternative, evolutionary conserved circuits - such as the dorsal pallium and basal ganglia (Naumann et al., 2015) - to support social timing.

Third, predictions on timing abilities can be made for and tested in other mammals based on their sociality and phylogeny, ultimately leading to the refinement of the Socio-Temporal Brain hypothesis. For instance, rats or sea lions show greater social structure and complexity than dormice or harbour seals. The original Socio-Temporal Brain hypothesis predicts that enhanced social complexity correlates with enhanced timing capacities (Schirmer et al., 2016). Accordingly, a “Comparative Socio-Temporal Ganglion” framework would predict rats or sea lions to exhibit a more developed timing repertoire than dormice or harbour seals. In particular, if this hypothesis is correct, social timing might greatly differ between closely related species, which have different degrees of social complexity. At the same time, non-social timing should exhibit similar characteristics in closely related species no matter their social differences, due to common ancestry. In a similar framework, and more generally, one could conceptualize sociality and timing as two traits, and test whether these co-evolved.

Fourth, isochronous synchrony has received the most scientific attention to date, but this is just one of the many forms of coordinated social behaviour in time. Other timing patterns beyond synchrony should be investigated across species and domains. For instance, antiphonal chorusing as observed in wrens (Mann et al., 2006), or the patterns of 'contagious' howling in wolves (Harrington, 1987), might prove as interesting as perfectly synchronous behaviour (Ravignani et al., 2014; Ravignani & Cook, 2016). In brief, the original Socio-Temporal Brain hypothesis proposes a mutual modulation between timing and sociality: Extending the hypothesis to non-human animals will unveil how the link between timing and sociality emerged in animal evolutionary history.

Comparability of results will be crucial in cross-species research, requiring, in turn, a cross-disciplinary quantitative framework to guide empirical work. This framework should be developed by unifying knowledge of social timing across all taxonomic groups and species (including humans), and linking neural circuits with social interaction via individual timing patterns. In particular, it should systematically compare four dimensions across species: (A) neural processes, which underlie (B) different cognitive mechanisms (predictive, reactive, etc.) producing (C) various individual timing patterns, which (D) shape and are shaped by group/social interaction. Such dimensions would connect neural processes to behaviour stepwise, with:

(A) a neural space, representing brain activity in e.g. vocal production/perception as the neural network involved and its oscillation frequency (Kotz & Schwartze, 2016);

(B) a cognitive space, representing whether timed behaviour is produced by reacting to previous events vs. forming a representation of future events vs. ignoring most temporal input, and whether reactive/predictive behaviour is adapted to internally-generated vs. externally-perceived events (Kotz & Schwartze, 2016);

(C) an individual production space, representing an individual physical variable in terms of its change over time. Physical signals can be vocalizations, visual displays, movements, and all other behaviours representable as an oscillatory signal for which timing plays a role;

(D) a group timing space, quantifying the relationship between physical signals generated by individuals in terms of their relative phase and relative oscillatory period.

Previous work can provide quantitative tools to refine and characterize each of the spaces (Chater & Vitányi, 2003; Kotz & Schwartze, 2016; Ravignani et al., 2014). For instance, two individuals vocalizing at similar rates (no matter the spectral properties of the signal) would show comparable frequencies in the group timing space (D). In the individual production space (C), this group coordination pattern would correspond to two sinusoidal waves, one per vocalizing individual, appearing entrained (Ravignani & Cook, 2016). This coordination pattern may result from at least two cognitive-behavioural mechanisms (space B): individuals could be attending to each other, predicting onsets and offsets of each other's calls, or they could just generate independent series of isochronous behaviours (Ravignani et al., 2014). Finally, the mutual prediction in the cognitive space may map to the neural space (A) via (in apes and speculatively) a cerebellar-thalamic network oscillating within the delta-theta range, namely groups of neurons in non-cortical brain areas slowly oscillating in synchrony at less than 10Hz (Schwartze & Kotz, 2016).

To summarize, we speculate that exciting work and discoveries await animal behaviour researchers interested in social timing. In particular, we argue that recent developments in human behaviour and cognition could inform and be informed by future work in animal research. In brief, we argue for the importance of testing (a) timing-dependent social behaviour, and (b) socially-modulated temporal behaviour.

Two outstanding lines of work we sketch above concern: (i) empirical data from particular species and (ii) an integrated, comparative theoretical framework. Empirical data from corvids and other songbirds, pinnipeds and other carnivores that show contagious chorusing behaviour, crustaceans, and primates might be particularly useful to relate timing, social behaviour, and the underlying nervous system. In parallel, a comparative theoretical framework would help mapping similarities and differences in (social) timing patterns across species, and help building 'phylogenetic timing trees'. We hope that our suggestions for experiments and our sketch of a quantitative, comparative framework will be useful to the animal behaviour community.

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References

Backwell, P., Jennions, M., Passmore, N., & Christy, J. (1998). Synchronized courtship in fiddler crabs. *Nature, 391*(6662), 31-32.

Bostan, A. C., Dum, R. P., & Strick, P. L. (2010). The basal ganglia communicate with the cerebellum. *Proceedings of the national academy of sciences, 107*(18), 8452-8456.

Chater, N., & Vitányi, P. M. (2003). The generalized universal law of generalization. *Journal of Mathematical Psychology, 47*(3), 346-369.

Enard, W. (2011). FOXP2 and the role of cortico-basal ganglia circuits in speech and language evolution. *Current opinion in neurobiology, 21*(3), 415-424.

Fitch, W. T., Huber, L., & Bugnyar, T. (2010). Social cognition and the evolution of language: constructing cognitive phylogenies. *Neuron, 65*(6), 795-814.

Greenfield, M. D., & Roizen, I. (1993). Katydid synchronous chorusing is an evolutionarily stable outcome of female choice. *Nature, 364*(6438), 618-620.

Gu, B.-M., van Rijn, H., & Meck, W. H. (2015). Oscillatory multiplexing of neural population codes for interval timing and working memory. *Neuroscience & Biobehavioral Reviews, 48*, 160-185.

Harrington, F. H. (1987). Aggressive howling in wolves. *Animal Behaviour, 35*(1), 7-12.

Hoshi, E., Jean, F., Carras, P. L., & Strick, P. L. (2005). The cerebellum communicates with the basal ganglia. *Nature neuroscience, 8*(11), 1491.

Kahn, A. T., Holman, L., & Backwell, P. R. (2014). Female preferences for timing in a fiddler crab with synchronous courtship waving displays. *Animal Behaviour, 98*, 35-39.

Kotz, S. A., & Schwartze, M. (2016). Motor-Timing and Sequencing in Speech Production: A General-Purpose Framework. In G. Hickok & S. L. Small (Eds.), *Neurobiology of Language* (pp. 717-724). San Diego: Academic Press.

Mann, N. I., Dingess, K. A., & Slater, P. (2006). Antiphonal four-part synchronized chorusing in a Neotropical wren. *Biology Letters, 2*(1), 1-4.

Matthews, J., Rendell, L., Gordon, J., & Macdonald, D. (1999). A review of frequency and time parameters of cetacean tonal calls. *Bioacoustics, 10*(1), 47-71.

Naumann, R. K., Ondracek, J. M., Reiter, S., Shein-Idelson, M., Tosches, M. A., Yamawaki, T. M., & Laurent, G. (2015). The reptilian brain. *Current Biology, 25*(8), R317-R321.

Pope, D. S. (2000). Testing function of fiddler crab claw waving by manipulating social context. *Behavioral Ecology and Sociobiology, 47*(6), 432-437.

Ravignani, A., Bowling, D. L., & Fitch, W. (2014). Chorusing, synchrony, and the evolutionary functions of rhythm. *Frontiers in psychology, 5*, 1118.

Ravignani, A., & Cook, P. (2016). The evolutionary biology of dance without frills. *Current Biology, 26*(19), R878-R879.

Rilling, J. K. (2014). Comparative primate neuroimaging: insights into human brain evolution. *Trends in cognitive sciences, 18*(1), 46-55.

Ryan, M. J., & Rand, A. S. (1999). Phylogenetic influence on mating call preferences in female túngara frogs, Physalaemus pustulosus. *Animal Behaviour, 57*(4), 945-956.

Schirmer, A., Meck, W. H., & Penney, T. B. (2016). The Socio-Temporal Brain: Connecting People in Time. *Trends in Cognitive Sciences, 20*(10), 760-772.

Schwartze, M., & Kotz, S. A. (2016). Contributions of cerebellar event-based temporal processing and preparatory function to speech perception. *Brain and language, 161*, 28-32.

Sismondo, E. (1990). Synchronous, alternating, and phase-locked stridulation by a tropical katydid. *Science, 249*(4964), 55-58.

Yu, L., & Tomonaga, M. (2015). Interactional synchrony in chimpanzees: Examination through a finger-tapping experiment. *Scientific reports, 5*.