



Review

# The evolution of social timing

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## Abstract

Sociality and timing are tightly interrelated in human interaction as seen in turn-taking or synchronised dance movements. Sociality and timing also show in communicative acts of other species that might be pleasurable, but also necessary for survival. Sociality and timing often co-occur, but their shared phylogenetic trajectory is unknown: How, when, and why did they become so tightly linked? Answering these questions is complicated by several constraints; these include the use of divergent operational definitions across fields and species, the focus on diverse mechanistic explanations (e.g., physiological, neural, or cognitive), and the frequent adoption of anthropocentric theories and methodologies in comparative research. These limitations hinder the development of an integrative framework on the evolutionary trajectory of social timing and make comparative studies not as fruitful as they could be. Here, we outline a theoretical and empirical framework to test contrasting hypotheses on the evolution of social timing with species-appropriate paradigms and consistent definitions. To facilitate future research, we introduce an initial set of representative species and empirical hypotheses. The proposed framework aims at building and contrasting evolutionary trees of social timing toward and beyond the crucial branch represented by our own lineage. Given the integration of cross-species and quantitative approaches, this research line might lead to an integrated empirical-theoretical paradigm and, as a long-term goal, explain why humans are such socially coordinated animals.

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## 1. Introduction: what is social timing?

The term “social timing” refers to the rather intuitive notion that sociality and timing are tightly interrelated in inter-individual interaction: for example, some bird species engage in precise duets, where the partners’ vocalisations can either overlap or alternate with extreme temporal precision [1]; similarly, a human conversation flows based on the unwritten rules of timely turn-taking, and crowds at concerts spontaneously synchronise their movements and voices

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[2,3]. In contrast to other instances of coordinated timing (e.g., with a metronome, with an external sound source like music), social timing is a dynamic phenomenon of mutual adaptation in time between two or more agents. This coordination supports behaviours necessary for survival, but also rewarding and communicative acts [4]. Under this broad umbrella term, we can thus include several instances of coordinated timing [5], from chorusing to turn-taking and from music playing to courtship behaviour [6,7]. While these diverse situations highlight the ubiquity of social timing, they also display the challenges we face in trying to harness it: is it possible to reconcile the finesse of a pleasurable musical ensemble with the primary need for mating under the same conceptual hooding? To answer these questions, we propose a comparative framework: the study of social timing abilities in a broad range of animal species will help unveil the evolution of social timing and reveal the common ultimate functions behind apparently diverse proximate functions (see Table 1; [8]).

Social timing, as defined here, may allow embracing a comparative perspective and reconciling some of the inconsistencies emerging from previous research. To achieve this aim, social timing should be conceptualised and operationalised in ways that are directly applicable to non-human animals, thus expanding previous propositions built predominantly around humans, such as the Socio-Temporal Hypothesis [9]. Schirmer and colleagues (2016) discussed the existence of a bi-directional interaction between social and individual timing. While the authors acknowledged the existence of temporal coordination in other species, their proposition remained human-centred. For example, the proposed neurobiological underpinnings included the striatal beat frequency model, which primarily accounts for cortical oscillatory activity (e.g., [10]). However, this model effectively excludes numerous species that lack a cortex while still displaying clear and complex social timing behaviour, such as fireflies, ants, and bees (e.g., [11]).

Further, existing literature is often unclear about what is meant by “sociality” and “timing” (or combinations thereof), with divergent operational definitions across domains and species. For example, sociality has been defined as a function of either pair-bonding and group size (e.g., [12]) or, more loosely, as the interaction between agents with a communicative intent [9], often dependent on brain size ([13,14]; but see [15] for a different viewpoint). It is unclear whether these definitions apply to dyads, groups, or both, but also how the biology of different species may factor in: from a comparative angle, several of these definitions exclude some species a-priori [6]. For instance, what is the communicative intent of a firefly? Do bees have a sense of agency? The lack of a dedicated framework complicates a better understanding of sociality, timing, and their shared evolutionary trajectory: Is social timing a highly conserved trait, common to many species, or does it derive from a recent evolutionary leap? If so, was this jump done by humans only, or is it shared with evolutionary close species such as other primates (e.g., [16])? Can we reconstruct the building blocks of social timing in living organisms with the help of artificial systems (i.e., agent-based models, robotics)? Here, we lay the necessary groundwork for answering these questions: we start by providing a wide-angle comparative review of the social timing literature, which we then use to elaborate on a novel framework including operational definitions, methods, and hypotheses that facilitate a comparative approach, mindful of the biology and characteristics of different species. We also suggest an initial, taxonomically diverse set of target species for subsequent research, selected based on their social and timing capacities.

## 2. Comparative social timing until now

### 2.1. Does social timing exist in non-human animals?

To some extent, all animals can perceive time and interact with one another [17,18]. Indeed, mechanisms akin to social timing have been empirically shown in several species other than humans. Examples of species that display social timing include insects (fireflies: [19,20]; [21]; ants: [11]; bees: [22]), birds [23,24], and multiple mammalian species (e.g., bats: [25]; cetaceans: [26,27]; chimpanzees: [28]; macaques: [29]). Little is currently known about social timing in reptiles. This is not entirely surprising as reptiles are (in)famous for their purported lack of sociality [30]. Yet, some studies challenge this claim with evidence—in several reptilian species—of socially relevant skills, such as social learning [31] and gaze following [32,33]. These examples are noteworthy for multiple reasons: First, they highlight the need for systematic comparisons targeting not only species that have already received much attention (such as birds, primates, and humans), but also less studied and supposedly solitary species. Second, they show how even “non-social” animals can use social timing skills [34,35].

Social timing can serve different functions both *between* and *within* species. For example, synchronised swimming in cetaceans can have anti-predatory [26] and affiliative functions [36]. These examples underline the role of situational context in influencing both sociality and timing: for instance, in the presence of a predator an individual may

Table 1  
Glossary.

<i>Analogy</i>	Similarity between behaviours (or anatomical structures) across species, resulting from convergent evolution. Examples of analogous structures are the wings of bats and birds. They are analogous because their last common ancestor did not have wings, but similar pressures for flight resulted in similar structures.
<i>Homology</i>	Similarity between behaviours (or anatomical structures) across species, which existed in or derive from a common ancestor. Examples of homology are the tailbone in humans and non-human animals (e.g., cats, dogs, chimpanzee, etc.), or upper limbs in humans (arms and hands) and bats (wings)
<i>Convergent evolution</i>	Chain of changes and adaptations leading different species to acquire a similar trait not necessarily present in their common ancestor. It is often caused by similarity in the living environments or functional pressures; for example, aerial environments and a pressure for flying led to the independent development of wings in birds, bats, and some insects.
<i>Divergent evolution</i>	Chain of changes and adaptations leading closely related species to increase their diversity due to, for example, migration, food competition, or genetic mutations.
<i>Proximate cause</i>	An event, which constitutes a direct or closest cause for an observed phenomenon, such as the environmental or physiological factors impacting a given biological function.
<i>Ultimate cause</i>	An event, which constitutes the past or functional cause for an observed phenomenon, such as the evolutionary force shaping a given biological function.
<i>Time scale</i>	Basic unit of time that can be perceived or produced by a species

react by freezing (i.e., no observable change in behaviour is expected while the threat persists) or by finding safety in synchrony and numbers (e.g., schooling in fishes). This variability can occur both within- as well as between-species and can be used to gather information about the evolution of social timing: On the one hand, variability *within* individuals of a species provides the scaffold for natural selection to model social timing capacities. For example, if individuals characterised by advanced social timing skills also show higher than average reproductive output, then we might consider social timing as an adaptive behaviour favoured by sexual selection (see [37] and [38] for potential evidence in this direction). Furthermore, variability between groups of individuals within a species may contribute to defining social boundaries. For instance, human conversational turn-taking is characterised by universal features such as the avoidance of overlaps and the minimization of gaps between turns, which coexist alongside striking cultural preferences for gaps of different duration [39]. Whether such variations in social timing also exist in non-human cultures remains to be further explored. On the other hand, *between* species comparisons are necessary for several reasons. First, social timing behaviours that look superficially similar may serve completely different purposes, thus implying different evolutionary origins. For example, synchronised swimming has been observed in both killer whales [40] and beaked whales [26], but while killer whales use this as a hunting technique, beaked whales swim together to avoid predation. A comparative approach is then needed to differentiate between cases of social timing resulting from convergent or divergent evolution (see Table 1). Second, different species developed idiosyncratic ways to communicate depending on their habitat and ecology; for example, aquatic habitats make vocal communication more effective than visual communication. Therefore, the vocal capacity of aquatic mammals is particularly developed [13]. However, these two channels (acoustic and visual) are characterised by different time scales, and animals preferring either one or the other may communicate “at different tempi”. Similarly, visual communication may require proximity and close contact, thus limiting the number of individuals involved in the communicative process. These differences cascade into different timescales of behaviours as well as different nuances of what it means to be “social”. This evidence is often disregarded in favour of a rather anthropocentric theoretical and methodological approach. For instance, the typical human preference for timing around 600 ms is often employed in studies targeting non-human animals, regardless of each species’ specificity and temporal sensitivity [41]. These approaches affect the way different species are studied, and how their behaviours are interpreted, and stress the need for more comparative evidence.

## 2.2. Which mechanisms may support social timing?

While social timing seems to be a common trait across many species, its evolutionary trajectory is largely unknown, and so are the mechanisms supporting it. Different approaches have put forward alternative explanatory mechanisms, focusing on physiological, neural, cognitive, or emotional aspects as main drivers in the evolution of social timing. Each of these accounts predicts different relationships between timing and sociality, with either phenomena acting as a prerequisite, consequence of, or mutual reinforcer of the other (Table 2).

A particularly influential view relates social timing to the effect of synchronised neural activity, which facilitates social interactions by making the agents' behaviours mutually more predictable [42,43]. Neural synchronisation between interacting partners has been frequently observed not only in humans (for reviews see [44]; [45]; [46]), but also in rhesus macaques [47], Egyptian fruit bats [48,25], rodents [49], and birds [1]. However, the *causality* among social interaction, synchronised neural activity, and synchronised behaviour is not yet clear. Some authors propose that the coordination of brains is required for social interaction [25], yet this claim is currently only confirmed in a few species and extremely problematic to test in others (e.g., for example in insects due to size and/or ecology—but see [50,51] for recent advances in insects neuroimaging). Furthermore, new evidence from plants may significantly challenge this hypothesis (see Paragraph 5). While Omer, Zilkha, and Kimchi [52] advocate the use of tools such as microstimulation, optogenetics, or genetic manipulations (p. 273), we add that the use of ethorobots (i.e., social robots created by keeping in mind the rules of animal behaviour) might represent a non-invasive complement to explore social timing in a more naturalistic way. Indeed, the use of ethorobots may allow for more fine-grained testing of specific hypotheses by manipulating behaviours with extreme precision and in a controlled, yet ecologic environment.

Other accounts highlight physiology as a building block of temporal-social behaviour ([53]; see also [54,55]). Physiological responses are often expressed by repetitive patterns in time (e.g., rhythms) that are intertwined with social signals [56–58]: for example, heart rates synchronise between humans in a wide range of social contexts [59,60], banded geckos group together to reduce their evaporative water loss [61], and several other species show synchronised breathing especially in intense social contexts (cetaceans: [62,63,36,27]; fishes: [64]; birds: [65]). Interestingly, respiration and olfaction can carry social signals transmitted by neuropeptides—such as oxytocin and vasopressin—which are known to modulate social behaviour ([66,53]; but see [67] for a critical viewpoint on oxytocin). In turn, respiratory and olfactory rhythms can entrain brain activity [68,55,69], and modulate attention [70–73], social learning [35], and other cognitive functions. Thus, physiological rhythms and social context may influence each other [74,61].

Cognitive and psychological models stress the importance of mentalizing (Theory of Mind)—the capacity to track the intentions, desires, and beliefs of others ([75]; see also [76]). In this process, intrinsic motivation is a major force in interacting with others [77]. In line with these models, the recent self-domestication hypothesis puts pro-sociality and the early emergence of cooperative and communicative abilities at the centre stage of cognitive evolution [78]. While timing is not explicitly mentioned in these models (but see [79]), neurological conditions affecting Theory of Mind and social interaction (e.g., autism spectrum disorder) are associated with limited temporal processing capacities ([80,81]; but see also [82,83]). Yet, these psychological and cognitive models are typically human-based and are difficult to extend to other species.

It is important to note that these proposed mechanisms (i.e., neural, physiological, cognitive/psychological) are not mutually exclusive: as shown by the reciprocal influence between respiratory and neural rhythms, they mutually influence each other [68]. Due to this complex interaction, it is difficult to disentangle how and to what extent each mechanism specifically contributes to social timing. Furthermore, multiple mechanisms may have been adapted in response to different evolutionary pressures, acting on different species and resulting in convergent or divergent evolution of sociality and timing. Specifically, this implies that different constellations of mechanistic interactions may have led to similar outcomes across species. As we propose in the following sections, one way to overcome this issue is by systematically testing species that vary widely in their biological and cognitive capacities.

Table 2  
Summary of the main mechanisms hypothesized to support social timing.

Proposed mechanism	Sub-components	Challenges	Sociality-timing relationship
Neural activity	<ul style="list-style-type: none"> <li>• Frequency bands</li> </ul>	<ul style="list-style-type: none"> <li>• Non-invasive</li> <li>• Difficulties for small brains</li> <li>• Requires at least single neurons</li> </ul>	Timing → sociality
Physiology	<ul style="list-style-type: none"> <li>• Breathing</li> <li>• Locomotion</li> <li>• Heart rate</li> <li>• Hormonal system</li> </ul>	<ul style="list-style-type: none"> <li>• Extreme inter-species variability</li> <li>• Requires specific organs</li> </ul>	Sociality ↔ timing
Cognition	<ul style="list-style-type: none"> <li>• Theory of Mind</li> <li>• Motivation</li> </ul>	<ul style="list-style-type: none"> <li>• Testing in non-human animals</li> <li>• Intrinsic vs. extrinsic motivation</li> </ul>	Sociality → timing

### 3. A new framework for social timing: evolutionary bootstrapping

So far, we have reviewed evidence on social timing across species and the possible mechanisms supporting this capacity. We also identified several shortcomings that need to be addressed: Most studies focus on single-species and a single-methodology approach, while direct cross-species comparisons and multi-methodological studies are rare. In addition, comparative studies often adopt an anthropocentric viewpoint, both at the theoretical as well as the methodological level. To overcome these limitations, we propose a novel incremental framework to systematically compare human and non-human species characterised by varying social and timing capacities. The use of multiple methodologies will further allow exploring different possible mechanisms supporting social timing and their mutual dynamics. This approach should proceed in incremental small steps that allow testing progressively more complex and contrasting hypotheses on the evolution of social timing along a continuum between homology and analogy.

In the following, we outline a potential roadmap for applying this framework that hinges on four main points: i) basic operational definitions that can be applied to most species, ii) an initial set of representative test species, iii) feasible methods, mindful of each species' timescales and peculiarities and allowing to integrate different mechanisms (e.g., neural, physiological, behavioural), and iv) targeted research questions and hypotheses.

#### 3.1. Operational definitions

We conceive social timing as a dynamic phenomenon of *mutual adaptation in time* between two or more agents that supports rewarding communicative acts and/or acts necessary for survival. Under this broad definition, we can include several instances of coordinated timing, from synchrony (as in chorusing) to turn-taking [6]. In this sense, social timing is akin to “allelomimetic behaviour”, defined as “any behaviour in which animals do the same thing with some degree of mutual stimulation and consequent coordination” ([84] cited by [85]). Importantly, this definition reconciles phenomena occurring in different social contexts, both affiliative and aversive, that co-exist in all animal societies [86,54].

Within the broader umbrella term, the constituents “social” and “timing” still need to be defined in operational terms to index and quantify their corresponding behaviours. *Sociality* is often considered synonymous with social interaction—loosely intending the behaviours occurring when two or more individuals interact—and contrasted with isolation or solitary living (for example see [15]). A more complex spectrum is proposed in some disciplines, such as in research on insect behaviour and phylogeny. For example, Richards [22] draws from an extensive literature to code bee species according to five different classes of sociality: solitary, sub-social, social, eusocial, and hyper-social; the main distinction between these categories is the behaviour of the females during parturition, nesting, and upbringing of the prole. Richards' effort stems from the fact that numerous and often inconsistent definitions apply not only across related species, but also within taxa. Some authors stress the relevance of social behaviour for individual and group fitness ([87]; in humans: [88]; in baboons: [89]; in marsupials: [90]), mutual understanding [91], and individual recognition (in pinnipeds: [92]; in macaques: [93]). Among these, individual recognition based on visual or acoustic cues is often cited across species as an indication of social complexity [86]. Yet, tackling some of these aspects may be challenging, especially across species; for example, fitness is very difficult to gauge directly in long-living species, such as mammals [87]. Furthermore, indices of sociality vary: at the species level, they may include group size, group composition (ratio of females to males), and type(s) of social bonds [94,87]; at the individual level, they may incorporate overt social behaviours such as grooming and proximity (e.g., [89]), synchronised behaviour (for example, breathing in cetaceans: [63]; breathing in fishes: [64]; pecking in chickens: [85]), pair-bonding, male parental investment, and cooperation [95]. Often, these indices depend on the field of study; for example, cetaceans research frequently employs association (e.g., how often dyads are observed together; [96]). Across fields, a very simple and useful proxy for sociality is spatial proximity [85,97,89]: Individuals engaged in (especially affiliative) social exchanges tend to move closer in space. This basic measure can be used in small groups as well as in more complex settings, studying social networks with automatic techniques and in the wild. These methods allow distinguishing between spatial proximity due to true social interaction or simple spatial association; for example, in case of true social interactions individuals may cluster together in a non-random way (e.g., forming recurrent dyadic associations, possibly with a common goal), while spatial associations occur when individuals randomly cluster together in space and/or time without any preferred association and without getting any benefit from each other, but rather competing for available resources (in white sharks: [98]).

Regarding *timing*, we refer to the capacity to encode, decode, and process events—with a specific focus on their temporal dimension—and to temporally align with the environment [99]. Once again, this definition is rather broad but contains key elements that makes it applicable in comparative contexts: i) it covers both aspects of time perception (i.e., capacity to perceive and discriminate different time patterns and time durations) and time production (i.e., capacity to produce or reproduce temporal patterns); ii) it covers the capacity to dynamically adapt to changes in temporal patterns as a response to perturbations in the environment; iii) it refers to timing in the sub seconds-to-minutes timescale, as this is the most relevant for social interactions (see also [54]). While circadian and ultradian timescales are also relevant for social interactions (e.g., seasonal trends for courtship, mating, and birth cycles), they do not play a role in the fast rhythm of social exchanges and are not the focus here. We suggest that a comparative study of timing should at first establish basic timing capacities, such as preferred temporal rates and temporal discrimination thresholds. These measures are largely unknown in many species (see Table 3) but are crucial to construct species-appropriate paradigms and establish reliable baselines for inter-species comparisons [41,54]. Simple timing tasks may reveal surprising truths; for example, a visual time discrimination task showed that harbour seals possess a well-developed sense of timing and are capable of discriminating temporal durations partly in the milliseconds range [100–102]. While this series of studies did not test spontaneous time discrimination, they might guide further investigations of basic timing capacities.

### 3.2. Key test species

To facilitate future research, we propose a selection of representative species covering:

1. A spectrum of social capacities. For examples, we include prairie voles, a model species for high sociality [103] as well as several reptiles, which are considered solitary (non-social) animals.
2. A spectrum of (potentially) varied timing capacities. In this case, we include songbirds as a prime example for timing skills [104] as well as sloths, renowned for their slow timing. These timing capacities are based on time production rather than perception, as this is most easily observed in non-human animals (see paragraph 3.4.3 for details).
3. Species with potential to combine timing and sociality directly; for example, songbirds are well known for their capacity for social learning as well as for fine-grained temporal skills in vocal production ([23,105]; see also [106] for a review on vocal learning in non-oscine birds).
4. Species spanning different taxonomic levels; this is necessary to reconstruct the phylogeny of social timing and its evolutionary routes (convergent, divergent, etc.).
5. Species over a broad range of evolutionary distance from humans, to clarify whether social timing, as we define it, is a relatively recent adaptation, anciently rooted or convergently evolved.

Table 3 summarises, for each of these points, the available information on social and timing capacities in a selection of species that we deem particularly suited for comparative research on social timing. This list aims at providing a reasoned and reasonable steppingstone to test several important hypotheses on the phylogeny and evolution of social timing. Yet the list is not exhaustive and provides a broad overview, covering different modalities and effectors. Ad-hoc systematic reviews and meta-analyses targeting social and timing capacities within an order or class could also facilitate the identification of preferred time scales for specific forms of time (re)production (e.g., vocalisation or body movements).

### 3.3. Hypotheses

Several hypotheses can be formulated on the evolutionary trajectory of social timing in a multi-methodological space involving the mechanisms discussed above.

*Main hypothesis* – The main operational hypothesis on social timing can be formulated as a combination of null and alternative hypotheses. Under the **null hypothesis**, sociality and timing evolved independently with minimal reciprocal influence. This hypothesis predicts that we should be able to observe species with comparable social characteristics and different timing capacities, and vice-versa. The **alternative hypothesis** is that timing and sociality did not evolve independently; rather, at some point during animal evolution, they became functionally or mechanistically linked.

Table 3

Selection of species proposed to test social timing, reason for selecting them, and current knowledge of their social and timing capacities. For specific information on timing (sensorimotor synchronisation), also see [41]. The divergence time (evolutionary distance from humans) is reported as a median distance on published resources, calculated in the TimeTree website (<https://timetree.org/>). The scientific name is not indicated when i) we could not find literature on a specific species or ii) we assume inter-species differences to be negligible.

Species	Taxonomic order (class)	Rationale	Sociality	Timing	Estimated divergence time with respect to modern humans in million years (MM)
Chimpanzee <i>Pan troglodytes</i>	Primates (mammalia)	Proximity to humans	Highly social, aggressive, marked differences between sexes [107,108]	2.2–2.8 Hz (tapping; [109]; see also [110])	6.4 MM
Bonobo <i>Pan paniscus</i>	Primates (mammalia)	Proximity to humans	Highly social, reduced aggression [107,108]	4.6 Hz (drumming; [111]); 3–4 Hz (hooting; [112])	6.4 MM
White-handed gibbon <i>Hylobates lar</i>	Primates (mammalia)	Proximity to humans; timed vocal behaviour in duets	Unknown	3.1 Hz (male solo song; [38])	19.5 MM
Marmosets <i>Callithrix jacchus</i>	Primates (mammalia)	Relatively distant from humans, highly social, structured vocalizations	Highly social [113,95]	2 Hz (vocalisation; [114])	43 MM
Macaques <i>Macaca spp.</i>	Primates (mammalia)	Intermediate evolutionary distance from humans, highly social	Highly social [95] Sexual-social dimorphism (female form social bonds; [89])	5.7 Hz (teeth chattering) [115]	29 MM
Baboons <i>Papio spp.</i>	Primates (mammalia)	Intermediate evolutionary distance from humans, complex social structure	Complex social structure, multilevel society [116]	Unknown	29 MM
Zebra finch <i>Taeniopygia guttata / Taeniopygia castanotis</i>	Passeriformes (aves)	Model system for social learning	Highly gregarious, influenced by social context [117]	25–45 Hz (song pulse; [118])	319 MM
Red footed tortoise <i>Geochelone carbonaria</i>	Testudines (Reptilia)	Solitary reptile	Solitary animal, capable of social learning [31]	Unknown	319 MM

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Table 3 (continued)

Species	Taxonomic order (class)	Rationale	Sociality	Timing	Estimated divergence time with respect to modern humans in million years (MM)
Grainy Cochran frog <i>Cochranella granulosa</i> ( <i>Centrolenella granulosa</i> )	Anura (Amphibia)	Cooperative species, amphibian	Cooperative behaviour via acoustic alternation [119]	Unknown	353 MM
Panama cross-banded tree frog <i>Smilisca sila</i>	Anura (Amphibia)	Cooperative species, amphibian	Proposed cooperative behaviour via acoustic synchrony [119]	.03 Hz [119,120]	353 MM
Zebra fish <i>Danio rerio</i>	Cypriniformes (Actinopterygii)	Model of social cognition and social phylogeny	Highly social (visual), form groups in adulthood to avoid predation [121,122]	Max 9.5 cm/s swimming speed [123]	431 MM
Fiddler crabs	Decapoda (Malacostraca)	Visual social timing	Highly social, rich behavioural repertoire [124]	1.7 Hz (claw waving; [125])	694 MM
Crickets	Orthoptera (Insecta)	Group living insects, chorusing displays	Group living, establishment of social status without recognition [126]; stable social structure [127]	2.2–2.6 Hz (snowy tree cricket, stridulation; [128])	694 MM
Nematode <i>Caenorhabditis elegans</i>	Rhabditidae (Rhabditida)	Basic model, lacks respiratory or circulatory systems (useful to test physiology)	Food-related interactions: adult-larvae (oxytocin-dependent) and adult aggregation [129,130]	1.9 Hz (undulation frequency; [131])	694 MM
Aplysia <i>Aplysia spp.</i>	Gastropoda	Neuroscience model, few big neurons	Unknown, possibly solitary living [132]	0.5–1 s inter-stimulus interval for conditioning [133]	694 MM
Rat <i>Rattus norvegicus</i>	Rodentia (mammalia)	Neuroscience model	Social animals displaying several affiliative behaviours [134]	20–25 kHz / 30–80 kHz (ultrasonic vocalisation; [135])	87 MM
Mouse <i>Mus musculus</i>	Rodentia (mammalia)	Neuroscience model	Social animals displaying several affiliative behaviours [134]	8–12 Hz (sniffing; [136])	87 MM

Table 3 (continued)

Species	Taxonomic order (class)	Rationale	Sociality	Timing	Estimated divergence time with respect to modern humans in million years (MM)
Prairie voles <i>Microtus ochrogaster</i>	Rodentia (mammalia)	Social model	Monogamous, strong adult pair bonding [137]	Unknown	87 MM
Meadow voles <i>Microtus pennsylvanicus</i>	Rodentia (mammalia)	Contrasted with prairie voles	Polygynous [137]	Unknown	87 MM
Harbour seal <i>Phoca vitulina</i>	Carnivora (mammalia)	Known capacity for temporal discrimination	Mother-pup interactions, social play in pups, semi-solitary living [138]	Time perception (discrimination) similar to humans [100–102]	94 MM
Grey seals <i>Halichoerus grypus</i>	Carnivora (mammalia)	Direct comparison with harbour seals	Mother-pup interactions, social play in pups, group living [139,140,138]	Unknown	94 MM
California sea lion <i>Zalophus californianus</i>	Carnivora (mammalia)	Capacity to synchronise with external temporal stimuli [141]	Colonial living, displays synchronised swimming [142]	1–2.5 Hz (barking above or under water; [143])	94 MM
Sloths <i>Bradypus spp.</i>	Pilosa (mammalia)	Slow movements	Little known; <i>Bradypus variegatus</i> has solitary social structure [144]	Unknown	99 MM
Egyptian fruit bat <i>Rousettus aegyptiacus</i>	Chiroptera (mammalia)	Highly social, available neural data	Stable social groups, large colonies, familiarity discrimination [145]	20–100 ms time interval between click pairs [146]	94 MM

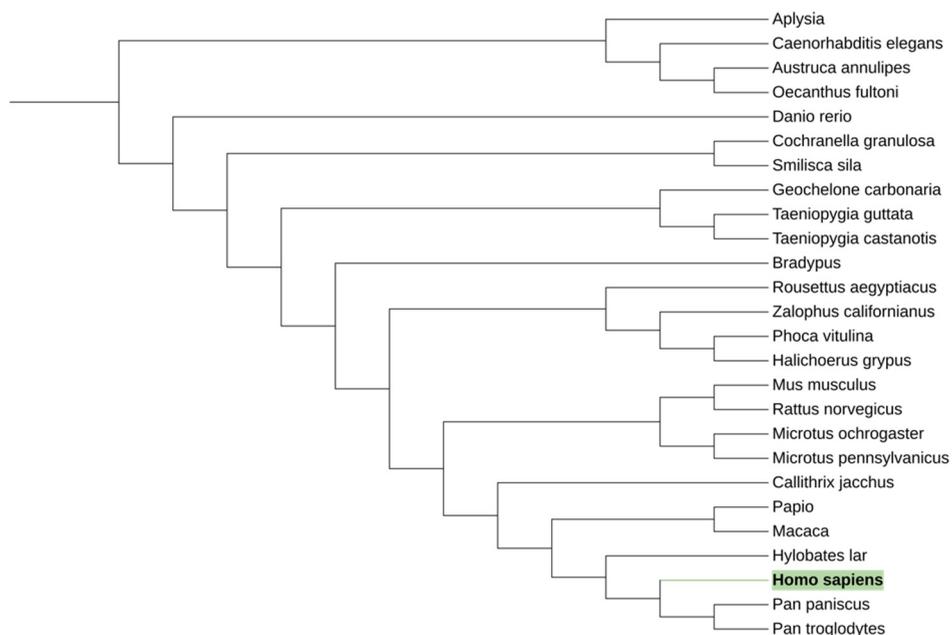


Fig. 1. Phylogenetic tree describing the relationships between the representative species described in Table 3 and including humans (*Homo sapiens*) as a reference point. Notice that the tree is unscaled: branch length does *not* encode divergence time or genetic divergence. As the literature on fiddler crabs and crickets focuses on different species, *Austruca annulipes* and *Oecanthus fultoni* were used here as examples (cited respectively in [125] and [128]).

Under this hypothesis, social species should outperform non-social species in their timing capacities; conversely, predominantly solitary (non-group living) species should have worse timing performances compared to social (group living) species. It is important to clarify that both sociality and timing are not intended as dichotomous categories; rather, each of them should be considered as a spectrum along which different species can be positioned based on their own capacities. In turn, this variability may inform the evolutionary pressures that moulded social timing in each species.

*Follow up research questions* – When rejecting the main null hypothesis, several follow-up options for alternative hypotheses arise (i.e., a co-evolution of sociality and timing). The logical next step would be to investigate ‘*when*’ and ‘*how*’ the coupling started. The proposed set of test species allows addressing the ‘*when*’ question: by targeting sociality and timing across distantly related species, an evolutionary scale can be added as an explanatory factor, allowing research questions related to the evolutionary pressures that enabled social timing to be investigated (i.e., convergent, or divergent evolution? see Table 1 and Figure 1). The ‘*how*’ question relates to the specific effect of single mechanisms (e.g., neural synchronisation, synchronised physiological responses) in the evolution of social timing. Is “optimal” social timing driven by one specific mechanism or does one mechanism predominate the other? We propose that the compound effect may be additive (i.e., “optimal” social timing is achieved when all mechanisms are in synchrony), but that inter-species variability may be rather large. For example, synchronised breathing seems to be a crucial factor in marine mammals, but it may be less relevant for other species.

### 3.4. Methodological suggestions

As previously mentioned, comparative approaches to social timing often suffer from methodological shortcomings, most notably by the adoption of an anthropocentric approach: in many studies, non-human animals are trained to produce a typically human behaviour, without considering their specific environment, behaviours, and capacities. We rather converge with other authors [41,54] in expressing a need to adopt an ecological approach to comparative studies. In the following sections, we provide methodological suggestions for researchers interested in this topic.

### 3.4.1. Observed behaviours

First, a naturalistic investigation of social timing should consider species-specific behaviours that the species is expected to naturally display in the absence of training or reinforcements. The rationale for this proposition is related to the evolutionary pressures that led to social timing, which are significantly altered when reinforcing a given behaviour in a laboratory setting. Thus, research conducted with rewards and computer testing (e.g., computer games and consoles; [147,148]), while extremely informative, tackles different questions and is beyond the scope of our proposed research line. This is not to say that research on social timing should be strictly observational: on the contrary, we propose that cross-species approaches should be complemented with those coming from mathematics, agent based modelling, and complex system sciences, to name a few ([149–152]; see also [153]). An example of this approach can be found in Ravignani [154], who tested several agent based models against empirical data to evaluate the timing capacities of harbour seals [155,156]. The model best describing the data corresponded to a seal pup adjusting her vocalisations to achieve a relative-phase anti-synchrony with other conspecifics' calls. This example reflects the importance of modelling for testing several alternative hypotheses against real empirical observations. In addition, nuances on potential mechanisms can be uncovered by using multiple, complementary approaches on the same data [155].

Importantly, modelling can facilitate testing both neural and non-neural models of behaviour, thus being potentially applicable to animal species for which the neural dynamics are unknown. For example, the behaviour of simple coupled oscillators [152,157] can be used to describe interactive dynamics at the neural level (e.g., Hebbian plasticity; [158]) and could represent an intriguing way to test higher-level social timing behaviour. At the group level, one can model individuals as single oscillators, and test whether the (known) social characteristics of the species correspond to the coupling strength among the single oscillators. Alternatively, techniques from game theory can be used to model strategic interactions among oscillators, to then study the resulting group timing pattern, for instance synchrony [159]. In general, we envision the need for a modelling framework that can encompass at least three complementary levels: 1) individual neural dynamics, 2) individual psychology and psychophysics, and 3) social cognition and group interaction [160,161]. Each of these explanatory levels could be or is already modelled with respect to its temporal dynamics. Ideally, a unified framework connecting all three levels could help integrate results and intuitions between contiguous levels. As suggested above, oscillatory models, such as the Kuramoto model, could work at these different scales [162]. Modelling formalisms could be used, rather than as statistical tools, to run simulations and explore the space of possible parameters at the three different descriptive levels.

Taking these suggestions one step further, we propose that sociality and timing can be empirically manipulated in inanimate subjects to confirm natural models (e.g., ethorobots; [163]; for a review: [164,165]). Ethorobots have been successfully employed to study social behaviours in several species, including zebrafish [166] and bees [167]. A main advantage of these methods is the ability to manipulate timing with extreme precision and under different contextual conditions (e.g., response to a predator, [168]). This latter point connects with the necessity to also consider each species' inherent capacities, preferred time scales, and contextual conditions [41]. This is a second advantage in these approaches, as opposed to computerized adaptive testing: interactions with ethorobots are embodied, with all the added naturalness this entails, and may better fit a species' perceptual and cognitive niche (e.g., [169]).

### 3.4.2. Experimental designs

To achieve a well-rounded understanding of social timing, we further propose a basic experimental design that can be replicated (with the necessary adjustments) across species. At a minimum, solitary behaviours should be contrasted with dyadic interactions; this basic unit can (and should) be stepwise enriched with group settings (e.g., more than three individuals), interaction with robotic agents, and mathematical modelling. The solitary condition is required to establish a baseline for timing behaviours (e.g., preferred spontaneous tempo), which can be contrasted not only with social conditions *within* a species, but also to evaluate timing capacities *between* species. Dyadic interactions are a natural next step, as dyads represent in many species a basic level of social interactions [86]. In dyads, timing is influenced by several contextual factors (e.g., leader-follower dynamics; in humans: [170]). Group settings reflect and amplify dyadic interactions, while further adding group-specific dynamics [86]. Thus, this extension would allow answering questions as to whether social timing, for a given individual, is influenced by the size of their social entourage. The contrast with ethorobots and mathematical modelling allows researchers to directly test multiple hypotheses and, in the case of robotic agents, has the inherent advantage of allowing a direct intervention of the behaviour under observation.

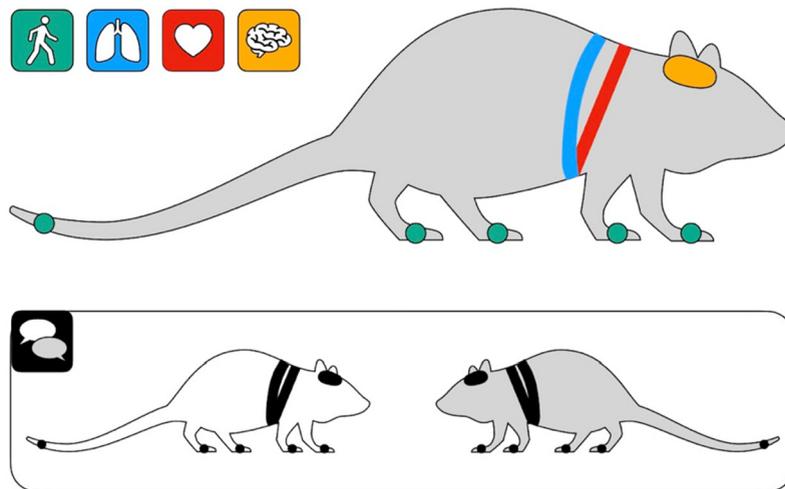


Fig. 2. **Multi-methodological social timing set-up in a representative species (mouse).** Multiple measurements should be collected to characterise the mechanisms underlying social timing in each species. Movement sensors (green) should be used to test for motion timing (e.g., gait speed); breathing (blue) and heart rate (red) can be measured with specific sensors to inform physiological rhythms; brain electrodes (orange) can track an individual's neural activity. In a dyadic setting, the same measures can be collected between two interacting individuals to inform on inter-individual synchronisation. Importantly, the figure depicts the maximum level of methodological complexity that should represent a final stage of incremental complexity from single-method settings.

### 3.4.3. Collecting data

How can we measure social timing, in a responsible comparative way, across species that have very little in common? We propose to start by targeting very basic social features and timing capacities. Concerning **sociality**, spatial proximity (i.e., the distance between two or more individuals) is a good candidate [85,97,89]. This basic measure can be i) easily obtained in experimental settings as well as in the wild, ii) measured in groups of different sizes, from very small to very large, and iii) easily complemented by mathematical models of social networks [171,116,172]. Similarly, **timing skills** should reflect a basic ability to perceive and (re)produce time as indicated by spontaneous motor tempo and sensorimotor synchronisation abilities. On the one hand, spontaneous tempo can be easily obtained in a species-specific approach from natural behaviours (such as walking gait, swimming stroke, pecking) in most species, including microorganisms like nematodes [173,174]. The characteristics make spontaneous tempo a promising baseline candidate for comparing timing scales and capacities across species. On the other hand, synchronisation abilities constitute the backbone of social timing, which is heavily based on the capacity to dynamically adapt in time. To measure this capacity, basic synchronisation measures (i.e., asynchronies, lagged correlations, beat synchronisation, etc.) should be collected [175]. In both cases, we propose that timing production—rather than perception—should be targeted, as it can be more easily obtained even from simple observation of natural behaviours, while time perception may require more complicated set-ups, for example involving reward-based training (but see [176] for a case of an experimental study not requiring external reward and [177] for a discussion of intrinsic reward in related contexts).

Lastly, to consider different mechanisms, the proposed measures should be complemented—in each sociality condition—by recordings of neural activity, physiological rhythms and (when possible) cognitive investigations into social capacities such as theory of mind [178], ideally simultaneously for multiple individuals (hyperscanning, see above; e.g., [25]). The simultaneous recording of neural, behavioural, and physiological data (Fig. 2) may shed light on the mechanisms preferentially used by each target species in response to environmental contingencies, but also on how different mechanisms organize dynamically to optimize behaviour [68,179]. Multi-methodological set-ups of this kind represent a higher level of investigation and require ad-hoc solutions for each species; for example, some animals, such as marmosets, can only be tested if unrestrained [95], thus requiring wireless methodology.

## 4. Feasibility and challenges

The adoption of a comparative framework to social timing presents remarkable challenges as it requires measuring the same parameters in species with different biological and environmental characteristics. While our proposition to

target basic skills aims at minimising this issue, there are at least two caveats. First, and foremost, differences between species hamper a systematic study of the mechanisms we identified as possible pillars of social timing. For example, neural synchronisation requires the presence of neuronal assemblies—if not entire brains (but see the next paragraph for a provocative perspective). However, this shortcoming can be used to further test evolutionary hypotheses on the relative contribution of different mechanisms to social timing; in other words: In the absence of a complex, organised assembly of millions of neurons, can we still see evidence for social timing? If so, what is the driving force? Research into “simple” organisms, such as *C. elegans* or *Aplysia spp.*, may be quite informative to answer such a basic question. Due to the simplicity of their neural and motor systems, these organisms are perfect candidates for modelling and testing specific hypotheses [180–182].

The second challenge is purely technical: some techniques, routinely employed in human studies, are not readily accessible for non-human animals. For example, non-invasive electroencephalography, a cornerstone of human neuroimaging, has been used with some success in a few species (such as cetaceans: [183–185]). Instead, for most species invasive recordings represent an easier alternative and are still preferred to this day (for example in pinnipeds: [186–188]). Despite their relative ease of use, these invasive methods are ethically questionable and have led in recent years to an increasing interest in the development of their non-invasive counterparts. For example, silicon cups have been used to cover external electrodes in cetaceans, allowing for non-invasive EEG recordings [189,184].

The last challenge is also an invitation to the broader scientific community: a comparative approach to social timing can only be effective with a large-scale collaborative empirical and theoretical effort across multiple disciplines and researchers. For example, systematic reviews and/or meta-analyses of social timing capacities focused on specific animal groups may jump-start experimental approaches, by providing a clear overview of which species have already been tested and which capacities they possess, while highlighting what remains to be targeted. Only in this way would it be possible to complete and expand Table 3, and to ultimately reconstruct accurate phylogenies of social timing—we suggest, one of the most widespread behaviours in nature.

## 5. Exceptional cases of social timing: cross-species and plant-based

While social timing within a species seems to be rather ubiquitous, very little is known about social timing between members of different species. A series of studies explored cross-species social interaction between domestic dogs and their owners and found evidence for synchronised behaviour (such as locomotion and gaze, both indoor and outdoor; [190–192]), and in response to unfamiliar objects [193]. Even more interestingly, and similarly to humans, dogs showed social preferences toward people who synchronise with them [190]. In wild (non-domesticated) animals, cross-species social timing has been observed within the primates’ order, especially between human and non-human primates. For example, capuchin monkeys, a highly social primate species, show a preference for humans who imitate the monkey’s actions [194], while bonobos show signs of tempo matching, entrainment, and synchronisation with a human experimenter in a joint drumming task [111].

While these examples testify that cross-species social timing may occur, at the moment they are limited to a few reports of interactions between our own species and others that are either evolutionary close (i.e., non-human primates), or that have been selected to live with humans, respond to their behavioural and emotional cues, and forge strong affiliative bonds with their owners (e.g., dogs, [192]; horses, [195]). This evidence invites several questions such as: how much similarity (or evolutionary closeness) is necessary for between-species social timing? This question has several implications concerning the proposed mechanisms and methods of study. In the already mentioned studies by Duranton and colleagues, the authors targeted locomotion to facilitate cross-species comparisons ([192]; see also [196]). Yet, what could be tested in an interaction between extremely distant species such as humans and fish? The possibility of time-based interaction in this case seems unlikely: because of the differences in their biological characteristics and ecological niches, it is difficult to imagine how members of evolutionary distant species could benefit from sharing time in their interactions. A different scenario emerges in the case of domestication and “forced sociality”, in which members of different species—for example humans and pet dogs—are forced to interact together in a shared environment. The effect of this on the development of social timing is unknown as the ability of pet dogs to synchronise with humans may be the result of genetic selection, of the evolutive and social pressure deriving from living with humans, or it may have been already present in a common human-dog ancestor (for a discussion: [190,192]). Studies on domestication of wild foxes begin to approach this question, by showing that social cognition in these canids evolved as a by-product of domestication [197]. It would be interesting to compare domesticated foxes with

both wild foxes and pet dogs, to clarify how these animals differ in their general timing capacities as well as in their capacity to synchronise with humans. Lastly, in all these cases, cross-species social timing occurs between humans and another species. Whether cross-species social timing can occur between two non-human species is a fascinating, albeit challenging, open question.

Another open question concerns whether social timing can occur outside of the animal kingdom: in proposing the evolutionary bootstrapping framework for social timing, we implicitly focused on *animal species* under the assumption that they should possess an albeit rudimentary nervous system to appreciate sociality and timing. Can this assumption be challenged? In recent years, several studies revolutionised established knowledge, by showing that action potentials, the basis of neural transmission, can be induced and measured in plants [198–200]. But can plants display social-like behaviours? Recent evidence completely overturned the idea of plants as passive living beings, by showing that they can interact with their surroundings and even respond differently to “kin” and “foes” [201–203].

Taken together, this cross-species evidence highlights even more the importance of social timing as a ubiquitous phenomenon. Yet, it also encourages to further reflect on its proposed mechanisms.

## 6. Conclusion

Social timing, the mutual adaptation in time of interacting agents, is a ubiquitous natural phenomenon. Decades of studies have demonstrated the pervasiveness of this phenomenon across human and non-human activities. However, where did it come from? To start answering this question, we have reviewed a set of separate literatures, describing phenomena that, albeit with different names, can be reconciled within the broad umbrella of social timing. We highlight the difficulties in tackling this topic from several angles and the various mechanisms proposed as building blocks of timely interactions. From this overview, we moved forward to advocate for a comparative naturalistic approach, necessary to build and contrast evolutionary trees of social timing towards and beyond the crucial branch represented by our own lineage. This approach should be systematic, yet flexible enough to consider each species’ biological and ecological characteristics. In addition, we discuss recent advances in robotics and modelling which should be an integral component of comparative studies, enabling the integration of cross-species and quantitative approaches. These suggestions and proposition should facilitate future research, ultimately leading to an integrated empirical-theoretical paradigm of social timing — an essential component of many life forms on earth.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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