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A comparative framework of inter-individual coordination and pair-bonding

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Inter-individual coordination (IIC) at the behavioral and physiological level, and its association with courtship and pair-bond maintenance, have been receiving increased attention in the scientific literature in recent years. However, there is no integrative framework combining the plethora of findings in humans and nonhuman species yet that addresses the evolutionary origins of IIC. Here, we take a comparative approach and review findings on the link between IIC and pair-bond formation, maintenance, and bi-parental care. Our review suggests that across socially monogamous species, IIC – at a behavioral and physiological level – is correlated with the likelihood of forming and retaining a pair-bond, and with reproductive success. We expand on the pair-bonding hypothesis by stating that higher levels of IIC might be beneficial for relationship quality and bi-parental care and, as a result, might also become a preferred trait in the formation and maintenance of a pair-bond. We further discuss the key questions to disentangle the evolution of IIC based on this hypothesis.

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Introduction

Human pair-bonding is characterized by a deeply emotional long-term bond.[5] Spending time with a significant other is associated with feelings of happiness [2], especially in committed relationships [3]. Such positive affect is an important characteristic of romantic bonds in humans, as it likely promotes the ultimate function of such bonds: motivating both parents to jointly care for their offspring [4]. However, the characteristics of a successful pair-bond and the fundamental prerequisites for successfully raising offspring remain not well understood. Nonetheless, the ultimate challenges faced by all species exhibiting bi-parental care are similar: raising and caring for their offspring, and crucially, dividing the tasks necessary for this goal. In this review, we outline a mechanism that might underlie successful relationship initiation, maintenance, and bi-parental care, namely inter-individual coordination (IIC). We present evidence suggesting that relationships that are or have the potential to be long-lasting might be characterized by IIC at both behavioral and physiological level, and that this pattern might extend to non-human species as well.

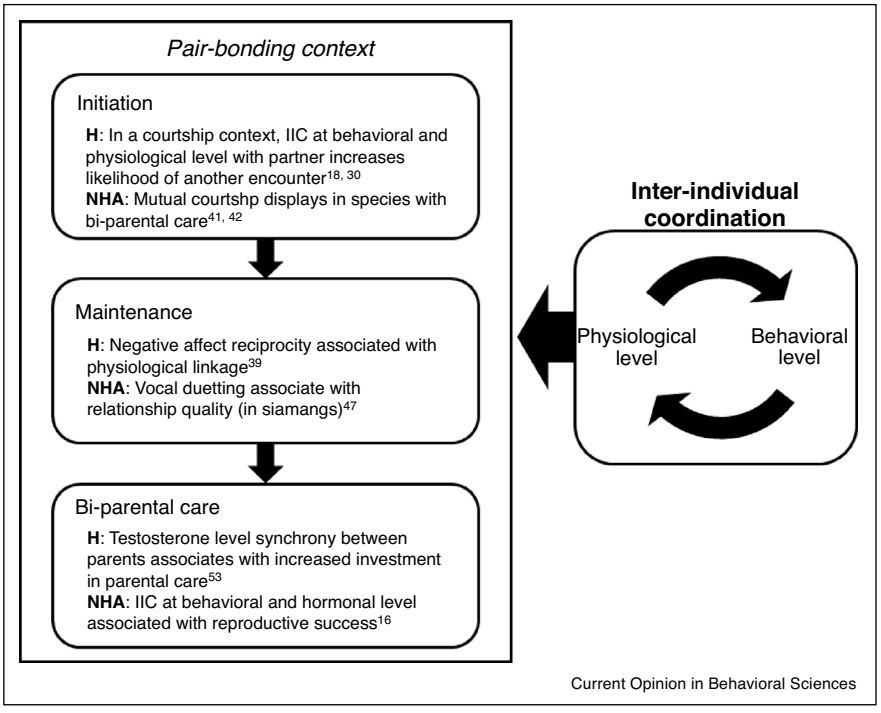
IIC refers to the behavioral and physiological linkage between two or more individuals [5•], and encompasses mimicry, synchrony [6], and complementary action [7].[6] Thus, while behavioral linkage mostly manifests itself externally (e.g., body posture), physiological linkage is mostly associated with co-activation and regulation of internal processes (e.g., autonomic nervous system responses). In this review, we define IIC as the co-variation of behavioral and physiological responses between two individuals that share a common goal. For example, while on a first date we feel nervous yet see our potential partner smiling, we might smile back and experience a decrease in nervousness and increase in happiness. In other words, we might coordinate with the person opposite of us both on a behavioral and physiological level. Figure 1 depicts how IIC is associated with different aspects of pair-bonding. For example, IIC facilitates bond formation in humans [8], and results in effective cooperation [9,10], a relevant component of bi-parental care. Accordingly, human courtship is strongly associated with IIC [11] and IIC has been implicated in relationship maintenance [12]. Thus, IIC might be a crucial element for successful bond formation and maintenance, and consequently, bi-parental care.

Non-human animals also show IIC [9], as can for example be observed in turn-taking [13] or facial mimicry [14].

[5] Here pair-bonding is not restricted to an *exclusive* assortment between one male and one female (e.g. social monogamy in cross-species research or monogamous marriage arrangement in human societies). Pair-bonds can refer to any lasting reproductive relationship between two individuals, including those in polyandrous and polygynous relationships [1].

[6] It should be noted that physiology and behavior are not independent, but rather embedded in a continuous feedback loop, where one level informs the other [5•].

Figure 1



Schematic representation of the effect of inter-individual coordination (IIC) on different stages of the pair-bonding process. Each stage contains an example from humans (**H**) and non-human animals (**NHA**).

Specifically, species with bi-parental care, such as many bird species, might be suitable models to study the role of IIC in relationship initiation and maintenance. Indeed, species with bi-parental care display IIC in mutual courtship behaviors, such as vocal duetting [15] and parental care [16••] (Figure 1). In this review, we outline evidence suggesting that IIC is prevalent in pair-bonding species and, from an adaptationist point of view, might confer reproductive benefits, such as more offspring or higher offspring survival. We set out to answer two main questions. First, how is IIC reflected in different components of pair-bonding (i.e. initiation, maintenance, and bi-parental care)? Second, how is IIC manifested on a behavioral and physiological level? Our goal is to integrate findings from psychology and ethology and create an inter-disciplinary framework for studying the role of IIC in pair-bonding.

Humans

Behavioral level

It is difficult to envision romantic interactions without coordination with a partner. Indeed, as outlined below, evidence shows that humans exhibit substantial IIC in the context of romantic love. In particular, patterns of behavioral coordination during first romantic encounters have been referred to as the human *courtship dance* [17]. For example, Grammer *et al.* describe a pattern of synchrony between couple members, where women, when interested in their partner, synchronize their movements with their partner [11]. Moreover, in a recent study [18••], participants were more interested in meeting a stranger again after engaging in synchronized activity together compared to a non-synchronized activity. Given that IIC is associated with shared intentionality [19], these findings suggest that IIC enables bond formation perhaps by facilitating the establishment of a common motivational framework.

IIC is also crucial in the maintenance of a pair-bond. Recently, Sharon-David *et al.* [20] demonstrated that participants who imagined having a synchronous interaction with their partner reported higher levels of intimacy in their relationship, while this was not the case for imagined out-of-sync interactions. Even more convincingly, Maister and Tsakiris [21] asked participants to perform one of two behaviors: either open or close their mouths. Simultaneously, participants were presented with pictures of their romantic partner or friends (as a control group) performing the same expression or not. Their results showed that participants imitated their romantic partner more often and faster than a platonic friend; suggesting that specifically romantic affiliation is more contingent on IIC. Crucially, similar evidence supports these findings based on real-life interactions: satisfied couples exhibited more movement coordination

compared to dissatisfied couples [22]. It is likely that these findings might also extend to emotional contagion, which is more prevalent amongst affiliated individuals [23]. For example, new parents that report higher relationship satisfaction are also more empathic towards each other [24]. Altogether, these findings suggest that IIC plays an important role in relationship maintenance.

Studies investigating bi-parental care and IIC in humans are at present limited. Two main patterns become apparent in the literature. First, marital satisfaction affects coordination within couples, and disruptions in coordination might consequently reduce paternal investment [25,26]. Second, decreases in paternal investment might reduce parental reciprocity [27], meaning that parental behaviors are more authoritative and less responsive to the infant's needs. Additionally, contexts where one parent undermines or does not support the other during parent-infant interactions might increase the likelihood of fearful temperament in the infant [28]. Thus, despite the limited number of studies and the complex triadic relationships, this preliminary evidence suggests that IIC affects bi-parental care, either directly or indirectly through marital satisfaction.

Physiological level

While behavioral IIC has received ample attention over the last decades, recent years have revealed a dramatic increase interest for physiological synchrony. Physiological synchrony is the co-activation and regulation of physiological processes, such as the autonomic nervous system and the endocrine system [5•,29]. In humans, physiological synchrony might be beneficial in facilitating pair-bond formation, as it might blur the boundaries between the self and the other and aid in establishing a shared perspective. Despite limited evidence regarding physiological linkage in couples over time, recent research [30••] has shown that heart rate (HR) and electrodermal activity (EDA) synchrony might be associated with increased attraction to an opposite-sex stranger. In conclusion, preliminary evidence suggests that physiological synchrony during courtship might influence its future prospects. However, more research is needed to investigate this complex relationship, especially the causality.

What do we know about physiological synchrony in couples? The different methodological and statistical approaches make this topic difficult to examine [31]. The level of physiological synchrony exhibited in a couple might be influenced by physical and emotional closeness [32,33]. Therefore, it would be logical to assume that more linkage occurs in a long-term relationship. However, whether this increased physiological synchrony is beneficial for a long-term relationship remains heavily debated. Previous research has shown that perspective taking ability and physiological synchrony are positively associated [34], which might support the notion that synchrony is beneficial in communication and consequently maintenance of a romantic bond.

Accordingly, emotional responses seem to align in couples over time [35]. This pattern, however, is complex and requires further empirical investigation [36]. This is also reflected in studies on physiological synchrony. Studies focusing on the sympathetic nervous system (SNS), a measure of arousal, during conflicts have shown counter-intuitive results. In their study, Levenson and Gottman [12] showed that couples exhibiting more SNS synchrony during conflicts reported lower marital satisfaction. Similarly, a recent study demonstrated that SNS linkage is related to a greater degree of demand-withdraw behavior during conflict [37]. These findings suggest that synchrony in negative contexts is detrimental to relationship maintenance. However, this assumption might be premature. Research has demonstrated that a 'regulatory linkage' strategy, whereby when one partner is negatively aroused the other downregulates their physiological response, might be more beneficial in de-escalating and resolving conflicts than a positive co-activation of the SNS [37,38,39••].These findings reflect the complexity of investigating physiological synchrony and relationship maintenance.

Non-human animals

Behavioral level

There are many examples of IIC that highlight its link with the formation or maintenance of pair-bonds, such as courtship displays in birds. Specifically, recent evidence demonstrates that familiar dyads of zebra finches (*Taeniopygia guttata*) that had been briefly separated showed stronger IIC after being reunited than novel dyads [40]. There are similar examples illustrating the importance of mutual courtship displays for initiation or maintenance of the pair-bond [41–43]. Crucially, successful coordination has been linked to pair-bonding and fitness [16••]. For example, well-coordinated pairs might be more successful in territorial defense and reduce offspring predation risk by synchronizing nest visits. A clear example of the importance of behavioral compatibility is provided by Ihle *et al.* [44•], who found that zebra finch couples that showed a mutual mate preference had a 37% higher reproductive success than experimentally 'forced' pairs. Crucially, individuals of mutually chosen pairs were staying closer together and showed more synchronous behavior. Importantly, this design allowed the authors to isolate the effect of parental care while controlling for genetic quality of offspring and parents, thereby convincingly demonstrating the importance of IIC in bi-parental care. Corroborating evidence comes from graylag geese (*Anser anser*), where reproductively unsuccessful pairs lacked coordination [45]. Also, blue-footed boobies (*Sula nebouxii*) that have been together for a longer time produce more fledglings, even when controlling for experience [46].

Importantly, the authors suggest that increased within-pair coordination over time could be the mechanism underlying this difference in reproductive success. Altogether, these examples illustrate that IIC can enhance reproductive output in birds.

In the past century, similar evidence has been shown for non-human primates. In general, coordination is more apparent in affiliated individuals [13,14]. Many primate species with bi-parental care are characterized by their duetting behavior, a clear example of IIC. Importantly, such duets seem to be restricted to pair-bonding primate species [15]. A famous example concerns siamangs (*Symphalangus syndactylus*), where duration and intensity of duetting correlated with relationship quality [47]; suggesting that the stronger the relationship, the smoother the song. Recently, these findings were extended to facial mimicry in gibbons: pairs with strong facial mimicry had a greater relationship quality [48•]. Importantly, the direction of causality is not clear yet. It is likely that IIC and pair-bond strength are embedded in a feedback loop; however, further research is needed to examine this notion.

Physiological level

Few studies have investigated physiological synchrony in non-human animals, and data in pair-bonding contexts are especially rare. This also applies to studies investigating physiological synchrony on a moment-to-moment basis [49], mainly due to methodological challenges. The few studies that investigated pair-bonding species and physiological synchrony have established that pairs synchronize on a hormonal level. For example, dyadic bond strength is associated with oxytocin synchrony in common marmosets (*Callithrix jacchus*) [50], and concentrations of hormones correlate in pairs of multiple bird species [16••]. Hormonal synchrony is crucial during mating periods because the hormonal state of one partner might induce courtship behavior, consequently changing the hormonal state and behavior of the other [51,52]. Comparable patterns have been found in humans, where men whose testosterone levels correlate with their partner's during pregnancy are more involved in raising their child and maintaining their relationship [53]. Thus, this preliminary evidence suggests that hormonal synchronization is relevant to establish a successful pair-bond and successfully care for offspring across species.

The pair-bonding hypothesis

Here, we have reviewed the literature on pair-bonding and IIC in humans and non-human animals. Our brief review suggests that IIC between partners might be a fundamental prerequisite for pair-bonding initiation, maintenance, and most likely, bi-parental care. Crucially, this prerequisite seems to be deeply rooted and extends beyond humans. Similar to humans, some animal species are faced with ultimate challenges relating to bi-parental care and relationship maintenance, such as producing, defending, and providing for their offspring together. All these challenges are easier to address when behavior is well-coordinated. Thus, when investigating the origin of partner bond-related behavior in humans, we should not overlook data from species facing similar challenges, namely raising offspring while relying on another individual. Therefore, we posit that a comparative framework integrating IIC and pair-bonding provides exciting opportunities to study the adaptive value of IIC in romantic relationships.

Here, we re-introduce and build upon the *pair-bonding hypothesis*. This hypothesis suggests that in species with bi-parental care, pair-bond strength is crucial for successful breeding [54]. While Rasmussen [54] refers to only the relationship between pair-bond strength and reproductive output, we specifically suggest that IIC could be the underlying mechanism. First, IIC and pair-bond strength might form a positive feedback loop, so that coordination between individuals increases and the pair-bond can stand the test of time. Increased IIC might in turn improve reproductive output because of improved offspring care; however, sustaining the existing pair-bond in itself might also be beneficial. Indeed, divorcing may bear reproductive consequences, such as the need to search for a new partner. Second, IIC might mainly function to set a high baseline pair-bond strength during initial stages of bonding, so that only well-coordinated couples will be established. Although not mutually exclusive, the first explanation is well-supported by literature showing that reproductive success and IIC increase over time [46,55].

The idea that IIC plays a pivotal role in pair-bonding and reproductive success of a pair results in three main predictions. First, in species with bi-parental care, IIC should be apparent during courtship, because high amounts of IIC are necessary to successfully raise offspring. Second, well-coordinated pairs that perform coordinated displays should have a stronger and more durable pair-bond than other pairs. Third, well-coordinated pairs should have higher reproductive fitness (reflected in either more offspring or higher survival rate) than pairs that are not well-coordinated. These predictions can for example be studied using cross-over designs [56]. In Table 1, we outline a few options to investigate these questions in both humans and non-human animals. For example, pair-bond strength can be quantified by incorporating measures of proximity and grooming or allopreening [57,58]. Consequently, their relationship with coordination [e.g., synchrony; 45] can be investigated to understand whether between-pair variation in pair-bond strength is associated with between-pair variation in IIC. A comparative framework provides clear advantages to test these predictions, especially regarding reproductive output. Importantly, for both humans and non-human animals it remains to be established at what level the coordination will be present: behavioral, physiological, or both.

Table 1

Overview of research designs suitable for each pair-bonding stage for humans and non-human animals

Stage of pair-bond	Humans	Non-human animals
Initiation	*Speed-date paradigms* During speed dates, the daters' behavioral and physiological linkage can be measured and used to predict date outcomes	*Mate-choice arenas* In a mate-choice arena, one individual is confronted with multiple potential mates. Behavioral and physiological linkage can be measured and used to predict mate preference.
Maintenance	*Correlational studies* In a longitudinal setup, the behavioral and physiological linkage of couples can be measured (e.g., from the start of the relationship) and correlated with indicators of relationship satisfaction.	*Correlational studies* In a correlational setup, variation in relationship quality can be linked to variation in IIC, such as vocal duetting or mutual courtship displays.
Bi-parental care	*Correlational studies*	*Cross-foster studies*[a] In cross-foster studies, some eggs or offspring are removed from the nest of their biological parents and raised by surrogates. This allows one to study the effect of IIC while controlling for genetic quality of the offspring. Thus, the effect of parental IIC on parental care can be examined in isolation. For an example, see [44•,61]. *Cross-over/serial breeding studies*[b]
	In a longitudinal or cross-sectional setup, the behavioral and physiological linkage of couples can be measured (e.g., from the start of the relationship) and correlated with investment in bi-parental care and relevant measures of reproductive fitness (e.g., health or developmental measures).	In cross-over designs, individuals can be sequentially paired with partners with whom they vary in IIC. This within-subject design allows the study of the effect of parental IIC on parental care while controlling for individual quality of the parents. For an example, see Ref. [56]. *Correlational studies* In a longitudinal or cross-sectional setup, the behavioral and physiological linkage of pairs can be measured (e.g., from the start of the pair-bond) and correlated with investment in bi-parental care and relevant reproductive fitness measures (e.g., offspring quantity and/or offspring survival).

[a] In birds and some primate species (e.g., marmosets).
[b] In serially monogamous birds or primates.

The link between IIC and pair-bonding is a natural extension of previous work that links specific behavioral phenomena to pair-bonding. For example, Julian Huxley already reported on the function of courtship rituals in 1914. Huxley extensively studied courtship displays in Great Crested Grebes (*Podiceps cristatus*) and argued that coordinated actions and the resulting emotional synchrony functioned to strengthen their pair-bond [59, p. 516]: '*I believe that the courtship ceremonies serve to keep the two birds of a pair together, and to keep them constant to each other*'. Thus, Huxley explicitly proposed IIC as a mechanism for pair-bonding. A similar approach was taken to explain vocal duetting in birds [60]. The bottom line of these models is that performing coordinated displays helps the initiation of a new pair-bond, strengthens an existing pair-bond and in turn, improving the quality of bi-parental care. Thus, we have integrated both the notion that pair-bond strength is essential for reproductive fitness, and the notion that IIC is crucial for establishing and maintaining such a pair-bond. Furthermore, we illustrate that IIC itself might play a role in reproductive fitness.

Conclusion and future directions

To delineate whether and when IIC is adaptive in pair-bonding, it is crucial to compare humans to other animals. Therefore, interdisciplinary studies by biologists and psychologists are essential. Recent theoretical models integrating findings from non-human animals and humans [6,62] have highlighted the importance of IIC for affiliation. However, the challenges inherent to such research (e.g., subtlety of emotional cues [63]) illustrate the need to focus on other measures, such as responses of the autonomic nervous system. Autonomic responses (e.g., pupil size change, blushing, sweating) are linked to emotions and are not under voluntary control [6]. Previous research has shown that pupil size [49] and facial temperature [64] can be effectively used in research with non-human primates. These methods provide exciting opportunities to study physiological synchrony in non-human animals.

In the present review, we provided a comparative overview of the relationship between IIC and pair-bonding. We have outlined the relationship of IIC and pair-bonding, as well as bi-parental care. However, we did not find sufficient evidence to delineate the direction of causality. In other words, does IIC actually cause a stronger pair-bond, or do individuals that are compatible just show better coordinated behavior? An explicitly comparative approach [e.g., as in voles: 65] can be fruitful in answering this and many other questions such as, do closely related species that differ with regards to bi-parental care and pair-bonding also differ in the amount and contexts in

which IIC is occurs? Further development of comparative theoretical will allow us to explain IIC findings in humans and other animals and advance the understanding of this multi-faceted relationship.

Conflict of interest statement

Nothing declared.

CRediT authorship contribution statement

Tom S Roth: Conceptualization, Writing - original draft, Writing - review & editing. **Iliana Samara:** Conceptualization, Writing - original draft, Writing - review & editing. **Jingzhi Tan:** Writing - review & editing. **Eliska Prochazkova:** Writing - review & editing. **Mariska E Kret:** Conceptualization, Supervision.

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