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Behavioral synchronization and affiliation: Dogs exhibit human-like skills

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Abstract

Behavioral synchronization is evolutionary adaptive, fostering social cohesion. In humans, affiliation between partners is associated with a high level of behavioral synchronization; people show increased affiliation towards people who synchronize with them. Surprisingly, until recently, little was known about these phenomena at an interspecific level, which is, however, essential to better understand the respective roles of evolution and ontogeny. After presenting why dog–human dyads are a relevant biological model to study this field of social cognition, we review the recent findings about dog–human behavioral synchronization. We summarize recently published findings on behavioral synchronization and affiliation between dogs and humans. We also review results showing that genetic selection modulates behavioral synchronization propensity in dogs, emphasizing the role of genetic selection on dog's social behaviors towards humans. Finally, we discuss the possible evolutionary influences and proximate mechanisms of this phenomenon. We conclude that, as in humans, behavioral synchronization acts as a social glue between dogs and humans. After dogs' ability to use human-directional cues or to produce referential cues towards humans, we evidenced a new human-like social process in the dog, at the interspecfic level with humans.

Keywords Communication · Comparative cognition · Cognitive ethology

Non-conscious synchronized behaviors[1] are found in various species, among all taxa. Being synchronized with other individuals is a broad phenomenon divided in three parts (Louwerse, Dale, Bard, & Jeuniaux, 2012). First, the temporal part of synchronization, called temporal synchrony, is defined as switching actions at the same time (Duranton & Gaunet, 2015, 2016a). The actions can be identical or different—the important feature is the timing. Second, the behavioral part of synchronization, called activity synchrony (see also behavioral matching, social mimicry or allelomimicry), is defined as exhibiting the same behavior at the same time (Chartrand & Bargh, 1999; Chartrand & Lakin, 2013; Duranton & Gaunet, 2015, 2016a). Third, the local part of synchronization, called local synchrony, is defined as being at the same place at the same time (Duranton & Gaunet, 2015, 2016a; King & Cowlishaw, 2009). Here again, the actions can be identical or different—the important feature is the location. If only one or two parts are observed, it is still considered as behavioral synchronization (Duranton & Gaunet, 2016a; Louwerse et al., 2012).

Exhibiting nonconscious behavioral synchronization has been maintained through evolution as it provides various adaptive advantages. Within groups, it decreases the pressure of predation on offspring: reproductive synchrony enables offspring to increase their survival rates through predation satiation and active defense by the parents and/or other adults of the group (see Duranton & Gaunet, 2016a, for a review). Being synchronized with other group members also increases the effectiveness of antipredation strategies, both passive (with, e.g., collective movements, dilution effect) and active (with, e.g., defensive circles, or vigilance against predators; see Duranton & Gaunet, 2016a, for a review). Finally, being synchronized with groupmates increases social cohesion. Behavioral synchronization is essential for group living and is a prerequisite for group cohesion. When considering

[1] There are two different categories of behavioral synchronization: conscious synchronization, in which each partner is aware of adjusting his or her behavior to others so that it can lead to phenomena such as cooperation (see, e.g., Dávid-Barrett & Dunbar, 2012; Valdesolo et al., 2010), and nonconscious synchronization, when the interacting partners are not aware of being synchronized or synchronizing their behaviors with others (see Duranton et al., 2017a).

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this specific function of behavioral synchronization, one has to focus on location and behavioral states rather than specific activities (i.e., to focus on local and temporal synchronies) as social cohesion relies on individuals being active and inactive at the same time, staying close and moving to the same places, whatever the activities (see Duranton & Gaunet, 2016a, for details).

Synchronization of behaviors is not only present in groups of individuals; it also occurs between only two interacting individuals (Duranton & Gaunet, 2016a). Animals in pairs benefit from behaving in a synchronous manner, such as decreasing the cost of food searching, reducing predation risk, and maintaining pair bonds between the individuals. Even if observed in various species such as dolphins (Sakai, Morisaka, Kogi, Hishii, & Kohshima, 2010), birds (Gunnarsson, Gill, Sigurbjörnsson, & Sutherland, 2004) or orangutans (Ross & Menzler, 2008), the latter point has been mainly studied in humans. Human partners synchronize their behaviors in numerous daily situations: sitting side by side (Richardson, Marsh, Isenhower, Goodman, & Schmidt, 2007), walking together (van Ulzen, Lamoth, Daffertshofer, Semin, & Beek, 2008), or simply chatting together (Richardson, Dale, & Shockley, 2008). Dyadic behavioral synchronization is evolutionary adaptive for humans, as it contributes to communication between individuals by signaling convergence of inner states, and as it helps to foster relationships and social bonds between individuals and thus leads to prosocial behavior (see Duranton & Gaunet, 2016a, for a review). Interestingly, behavioral synchronization and affiliation are acknowledged to be bidirectionally linked in humans: Behavioral synchronization increases affiliation between partners, and the more two individuals are affiliated, the more they behave in sync (see Duranton & Gaunet, 2016a).

However, even if the ability to behave in synchrony and its links with affiliation has been extensively studied at the intraspecific level, very little is known about the same phenomenon between different species. Despite the great interest that scientists have shown in the observation of mixed-species groups, the existence of behavioral synchronization at the interspecific level has been little studied. Paukner, Suomi, Visalberghi, and Ferrari (2009) provided evidence that capuchin monkeys looked longer at and interacted more with a human synchronizing his behavior with them compared with a person who did not synchronize. The authors concluded that synchronization could occur and play a role in interspecific interactions, at least between humans and nonhuman primates (Paukner et al., 2009). However, the question concerning the existence of dyadic interspecific synchronization between primates and nonprimates still remained unstudied. Stable groups or dyads involving primates and nonprimate species are not very common, but we have proposed that the unique relationship of humans and dogs offers the perfect biological model to study interspecific behavioral synchronization (Duranton & Gaunet, 2015, 2016a).

Indeed, pet dogs exhibit unique skills predisposing them to the existence of behavioral synchronization with humans: They are sensitive to humans' emotional cues and are known to share strong affiliative bonds with their owners. They are sensitive to other dogs' and humans' direct as well as indirect behaviors, and they adjust their own behaviors accordingly (Duranton & Gaunet, 2015). For example, they are known to be skilled at using human social signals such as pointing at a target, gaze, and visual direction of attention (see Duranton & Gaunet, 2015, for a review). All these skills make dogs an adequate model to study behavioral synchronization with humans.

Evidence of dogs–human behavioral synchronization

To evidence interspecific behavioral synchronization between dogs and humans, one has to choose a situation that is part of both species' daily life and that plays a role for the interacting partners. The situation and the behaviors at play have to be easily identifiable and reproducible by both dogs and humans (which is difficult, owing to dogs' and humans' different body types and lifestyles). Based on these criteria, locomotor (walking) situations and synchronization of its linked behaviors between humans and dogs appear to adequate to investigate. Additionally, walking behavior has been once previously suggested to be a good model for the study of behavioral synchronization between dogs and owners (Kubinyi, Miklósi, Topál, & Csányi, 2003).

Duranton, Bedossa, and Gaunet (2017a) thus investigated whether, when allowed to move freely in an enclosed, unfamiliar space, pet dogs synchronize their locomotor behavior with that of their owners (see Fig. 1a). We found that pet dogs visibly synchronized their location with that of their owners

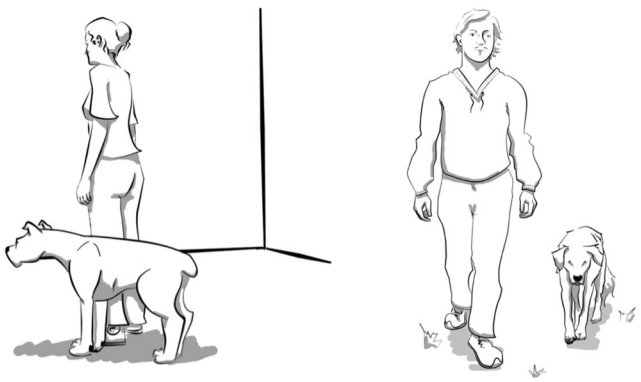

Fig. 1 Pet dogs synchronize all components of their displacements with that of humans indoor (left) and outdoor (right). Dogs exhibit local synchrony (they stay close and move to the same direction as their owner), temporal synchrony (they change from still to move, or move to still, when the owner changes), and activity synchrony (they are still when the owner is still, walk when the owner walks at a regular pace, and move fast—trotting or running—when the owner walks fast). Adapted from Duranton et al. (2017a, 2018a)

(staying in close proximity and moving to the same area), as well as their activity and temporal changes in activity (moving when their owner moved, standing still when their owner stood still, and gazing in the same direction as their owner). The study thus demonstrated the existence of dogs' behavioral synchronization towards their owners. We concluded that humans act as attractors for their dogs in an indoor space, as mothers do for their children (Campos et al., 2000; Clearfield, Osborne, & Mullen, 2008).

This study evidenced that dogs exhibit behavioral synchronization with their owners when walking indoors; it was indeed essential to study the existence of the phenomenon in a controlled and quiet place, as until then there was no evidence of the existence of dog–human nonconscious behavioral synchronization when freely moving. However, being alone in an empty room is not the most common situation for dog–owner dyads. Additionally, the testing room was an unfamiliar room, in an unfamiliar place for the dog–owner dyads. Even if dogs were given a 15-minutes period to explore and become acquainted with the place, and the authors controlled for stress (Duranton et al., 2017a), it is possible that dogs' reactions were different from their behavior in more familiar areas. To extend the knowledge of the cognitive properties of interspecies synchronization, investigating dogs' behavioral synchronization in more usual and familiar areas, in which dogs were used to move with their owners, was thus done when owners went for an outside walk with their dogs. Duranton, Bedossa, and Gaunet (2018a) therefore explored whether, when allowed to move freely in a familiar outdoor space, dogs synchronize their locomotor behavior with their owners' (see Fig. 1b). We found that dogs visibly synchronized both their location (staying in close proximity and going to the same direction) and their activity (moving when their owner moved, at the same pace, and standing still when their owner stood still) with that of their owners. By demonstrating that pet dogs also synchronize their behavior with their owners when freely walking in an outdoor familiar space, the authors evidenced that it is a robust phenomenon.

Finally, a related area of research recently investigated the existence of dogs' behavioral synchronization with humans. Social referencing, defined as the seeking of information from another individual to guide one's behavioral reaction (see, e.g., Merola, Prato-Previde, & Marshall-Pescini, 2012a; Duranton et al., 2016), was studied between dogs and humans in different situations. When facing an unfamiliar object, dogs synchronized their reaction with that of their owners: If the owners reacted in a positive manner, approaching the unfamiliar object, the dogs also approached it, whereas if the owners reacted in a negative manner, moving away from the unfamiliar object, then the dogs also avoided it and stayed as far as possible from it (Merola et al., 2012a). Similar findings of pet dogs synchronizing with the owners' locomotor reaction in social a referencing paradigm have been evidenced when the dyad is facing an unfamiliar person. The dogs' owners were instructed to behave in one of three ways towards the stranger: stay still, approach, or retreat. The dogs synchronized their reaction with that of their owners in the retreat condition (see Fig. 2), taking a longer time to approach the stranger, using their owners' reaction as the signal of a potential threat, and thus synchronizing with them (Duranton et al., 2016). These findings provide evidence of similar behavioral processes in dogs with their owners and human infants with caregivers (De Rosnay, Cooper, Tsigaras, & Murray, 2006; Duranton et al., 2016; Mumme, Fenald, & Herrera, 1996).

Behavioral synchronization is linked with affiliation between dogs and humans

In humans, the more two individuals are affiliated, the more they exhibit behavioral synchronization (Duranton & Gaunet, 2016a). Another essential aim of the present work was, as previously mentioned, to study the relationship between affiliation and interspecies behavioral synchronization. Domestic dogs, as a species, are divided into different subpopulations, such as free-ranging dogs, pet dogs, working dogs (e.g., police dogs, guide dogs), and shelter dogs (Duranton & Gaunet, 2016b; Udell, Lord, Feuerbacker, & Wynne, 2014). Each has different degrees and types of interaction with humans, which make dogs an appropriate model to study the effect of affiliation on interspecific behavioral synchronization. For example, the degree of behavioral synchronization with humans in pet dogs (living in human homes and having developed strong affiliative bonds with humans) can be compared with that of shelter dogs (who live in social isolation and are

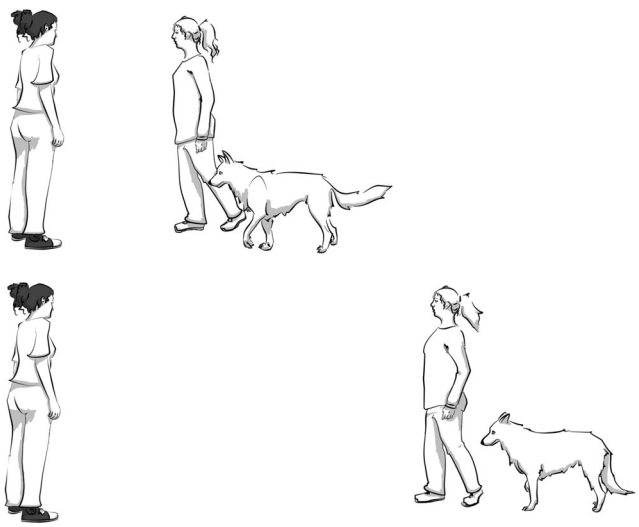

Fig. 2 When facing an unfamiliar person, pet dogs exhibit social referencing towards their owners based on the owners' displacement alone. When the owner is moving backwards (down), dogs take more time to approach the stranger compare to when the owner is moving towards the stranger (up). Adapted from Duranton et al. (2016)

deprived of extended contact with humans; see, e.g., Duranton & Gaunet 2016b for a review on the effect of shelter housing on dogs' social skills with humans).

Duranton, Bedossa, and Gaunet (2018b) have thus investigated if affiliation between the interacting partners affected the degree of behavioral synchronization when dogs and humans were walking freely outside. The authors conducted an experiment as similar as possible as of that in Duranton, Bedossa, and Gaunet (2018a), previously presented, but with interacting partners related by a weaker degree of affiliation: shelter dogs and their usual caregivers. After controlling for stress-related behaviors, results evidenced that shelter dogs exhibited less precise local synchrony (i.e., they spent less time in close proximity) with their caregivers compared with pet dogs with their owners, but they still exhibited mere local synchrony. Shelter dogs also exhibited activity and temporal synchrony (switching between being still, moving slowly, or moving fast), even if at a significantly lower degree than what is found between pet dogs and their owners (see Fig. 3). Such results evidenced the influence of affiliation on the degree of behavioral synchronization between two interacting partner of different species—dogs and humans—similarly to what is found among humans, as discussed in Duranton, Bedossa, and Gaunet (2017b).

Additionally, in humans, it is known that affiliation between the subject and the referent is important to observe social referencing: When the subject is not affiliated with the referent, she does not engage in social referencing (Zarbatany & Lamb, 1985; but see Klinnert, Emde, Butterfield, & Campos, 1986). To go further in the understanding of the role of affiliation in dog–human behavioral synchronization, it is thus relevant to observe its effect in a social referencing paradigm. Here again, the relationship between the dogs and the human referents has been found to be essential. Even if social referencing can occur between nonaffiliated dogs and humans, it is known that training experience modulates this propensity (Merola, Marshall-Pescini, D'Aniello, & Prato-Previde, 2013), and affiliation does play an essential role. Dogs better use referential reactions from familiar humans compared with humans they are not affiliated with (Merola, Prato-Previde, Lazzaroni, & Marshall-Peschini, 2014). When facing an unfamiliar object, dogs modify their behavioral reaction according to their owner's reaction and react very differently whether the owner's reacted in a positive or a negative way; but when the referent was a person the dogs were not

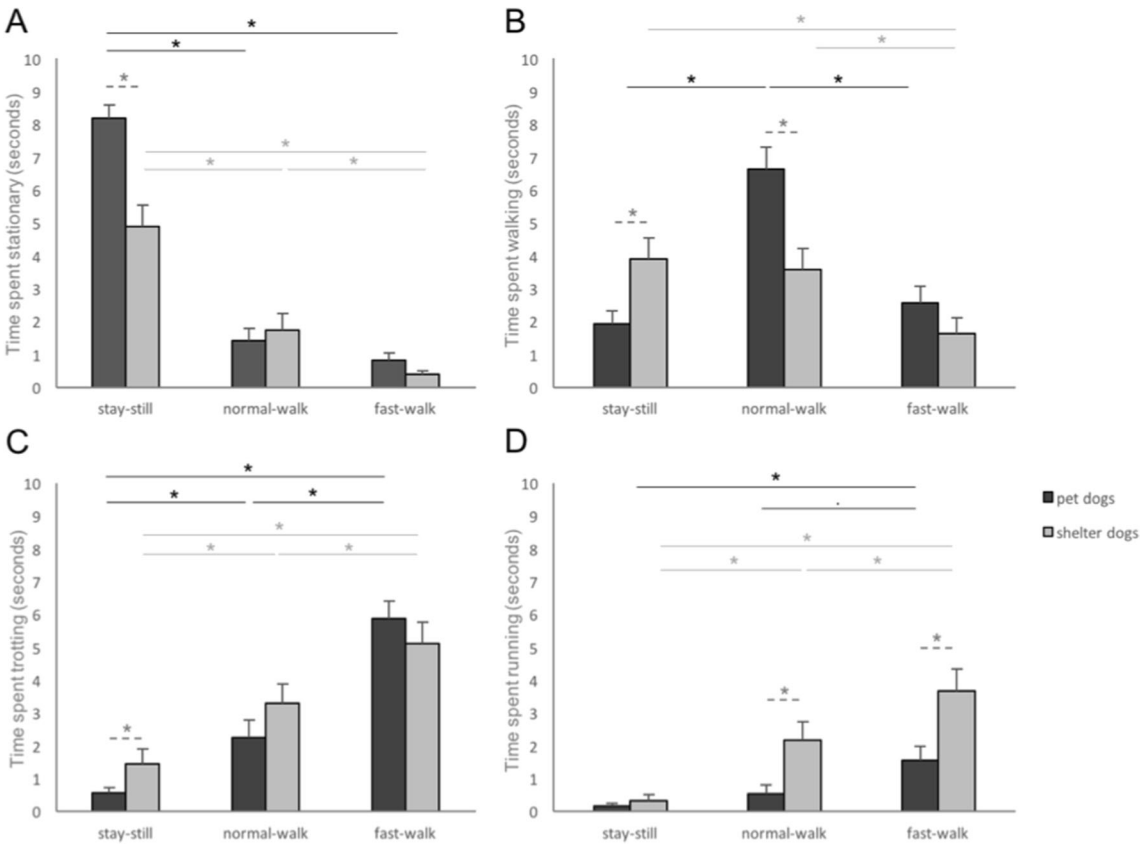

Fig. 3 Shelter dogs exhibit lower degree of behavioral synchronization with humans compared to pet dogs when walking outside. Time spent by the dogs performing different paces. Black bars and stars are for pet dogs, gray bars and stars are for shelter dogs, and green bars and stars are for the difference between pet and shelter dogs. *$p < .05$. Data used for the comparisons are from Duranton et al. (2018a, 2018b); and see statistics in Duranton (2017). (Color figure online)

affiliated with, dogs did not modify their behavioral reaction according to that of the referent (Merola et al., 2012b). Consistent with these findings, it has also been shown that when facing an unfamiliar person, shelter dogs do not engage in social referencing with their caregivers, contrary to privately owned pet dogs with their owners (see statistics in Duranton, 2017; Duranton et al., 2017b). These findings highlight the social deprivation that dogs in shelters are confronted with, and emphasize the importance of the affiliative bond between humans and dogs in creating social referencing.

Finally, in a last study, Duranton et al. (2018c) investigated the bidirectionality of the relation between affiliation and behavioral synchronization between dogs and humans. In humans it is known that people show greater affiliation with people who are behaviorally synchronized with them (see Duranton & Gaunet, 2016b, for a review), but little is known about the impact of synchronization at an interspecific level. If the more the dog–human dyads are affiliated, the more they exhibit behavioral synchronization, does it works the other way around? Does behavioral synchronization increase affiliation between dogs and humans? First, it is known that humans show increased affiliation for dogs who synchronize their behaviors with them (lying close to them, playing when they want to play; Protopopova & Wynne, 2014). Second, Duranton et al. (2018c) evidenced that synchronization of humans with dogs affects dogs' social preferences toward humans (see Fig. 4). When confronted with two unfamiliar persons, pet dogs exhibited social preference for the person who synchronized her locomotor activity with them (Duranton et al., 2018c). Behavioral synchronization is therefore a social glue in dogs, too: It is the first time that such a human-like skill has been highlighted in domesticated canids at an interspecific level.

Fig. 4 Pet dogs exhibit social preference towards people who synchronize with them. When encountering two unfamiliar persons, one synchronizing with them (up), one moving randomly (middle), pet dogs choose preferentially the synchronized person (down). Adapted from Duranton et al. (2018c).

Effect of genetic selection on behavioral synchronization skills in dogs

Domestic dogs as a species constitute a very relevant biological model for investigating the effect of genetic selection on social skills through the process of artificial breed selection. Dogs were originally used and selected for tasks they had to perform for humans, or at least that humans benefited from (King, Marston, & Bennett, 2012). To investigate the effect of genetic selection on behavioral synchronization, it is relevant to focus, for a first time, on breeds that were selected to be close to their owners, but which had been selected for different purposes. Shepherd dogs (also called herding dogs) and molossoid dogs (also called guard dogs) fulfill these criteria. Shepherd dogs have been selected for herding livestock and watching their owners during shared activities. Molossoid dogs were originally selected for guard work and for protecting their owners in novel situations. Both dogs are considered to be close to their owners (Eken Asp, Fikse, Nilsson, & Strandberg, 2015) and were selected to attend to humans' gestures and communicative cues, albeit to different ends (Svartberg, 2006; Svartberg & Forkman, 2002). These breeds should thus behave according to the temperament for which they were selected (Mehrkam & Wynne, 2014), and are thus appropriate to investigate whether genetic selection also affects shepherd and molossoid dogs' behavioral synchronization with humans.

In all of their studies investigating the existence of behavioral synchronization between dogs and humans, Duranton and colleagues compared performance of the two mentioned breed groups, shepherds and molossoids. Interestingly, breed never influenced the dogs' behavioral synchronization towards their human referent, whatever the condition. As soon as their owners started moving, the pet dogs engaged in high degree of behavioral synchronization (when walking inside: Duranton et al., 2017a; when walking outside: Duranton et al.,

2017b; when encountering an unfamiliar person, approach condition, and retreat condition: Duranton et al., 2016). Moreover, when shelter dogs displayed behavioral synchronization, we found no influence of breed group on their behavior (Duranton et al., 2017b). Two nonmutually exclusive hypotheses can explain these findings. It may be that when the owner moved, any potential breed differences are masked by the dogs' synchronization with their owners' behavior. This is consistent with the knowledge that both breed groups were selected to stay close to their owners. It is indeed likely that through domestication, dogs were all selected for their ability to engage in behavioral synchronization, to follow humans in their various activities, and thus both shepherds and molossoids have this inherited basis. It is, however, also possible that the situations in which we tested the dogs were too easy/basic or not challenging enough, or too far removed from the tasks for which the breeds were selected for behavioral differences to emerge. The above-described studies targeted basic/primary behavioral synchronization processes, and it is thus plausible to conclude that this level of social cognition is not sensitive to genetic selection.

However, when Duranton et al. (2018c) investigated dogs' sensitivity to human behavioral synchronization, they found a clear breed difference: molossoid dogs preferred an unfamiliar human who synchronized her behavior with them, whereas shepherd dogs did not. This finding is in line with a previous study showing that when owners are neutral, and do not provide any cues that could influence their dogs' behavior, pet dogs behave differently, according to the temperament for which their breed was selected during domestication, as previously mentioned (Duranton et al., 2016; Mehrkam & Wynne, 2014). Similar findings have been reported in human infants, as individual temperaments influence their behavior in social referencing paradigms (De Rosnay et al., 2006). Shepherd dogs were selected for herding livestock and focusing on their owners during shared activities. Molossoid dogs, by contrast, were originally selected for guarding work, where they had to attend to strangers. Studies of dogs' personalities have found that guarding breeds, including molossoids, are the boldest breed group (Starling, Branson, Thomson, & McGreevy, 2013; Turcsán, Kubinyi, & Miklósi, 2011), and notably bolder than shepherd dogs (Duffy, Hsu, & Serpell, 2008; Svartberg, 2006). Molossoid dogs were selected to cope with novel and unusual situations (Starling et al., 2013), whereas shepherd dogs are known to be more focused on their owners and less interested in unfamiliar people (see, for example, Duranton et al., 2016). It is thus plausible that, owing to selection through breeding, molossoid dogs are more interested in (and thus more sensitive to) the behavior of humans (unfamiliar persons) than are shepherd dogs, which explains why only molossoid dogs exhibited increased affiliation to unfamiliar people who mimicked them.

To conclude, an inherited basis acquired through domestication (i.e., form of genetic selection) can explain pet dogs' propensity to exhibit behavioral synchronization with humans. Additionally, it is relevant to assume that the genetic selection of dogs through breeding has resulted in differing degrees of sensitivity to human behavioral synchronization. Such assumption is in line with recent studies showing that genetic selection (through both domestication and breeding) affects dogs' human-directed social behaviors (Kis et al., 2014; Nagasawa et al., 2015).

Discussion

To sum up, the presented reviewed research revealed for the first time that dogs exhibit human-like behavioral synchronization skills. For instance, dogs' ability to use human-directional cues (Hare & Tomasello, 2005; Kaminski, Schulz, & Tomasello, 2012; Miklósi, Polgárdi, Topál, & Csányi, 1998) and to produce referential cues (Gaunet & El Massioui, 2014; Savalli, Ades, & Gaunet, 2014; Savalli, Resende, & Gaunet, 2016; Townsend et al., 2017) is a new human-like social process evidenced in dogs, at the interspecfic level. Being synchronized with other individuals is a prerequisite for avoiding misunderstandings about respective behavioral intentions, successfully managing interactions, and promoting social affiliation, and as a consequence, for learning contingencies in the social world (Ferrari et al., 2006). These benefits also apply to dogs. Behavioral synchronization has been referred to as a *social glue* in humans (Lakin, Jefferis, Cheng, &Chartrand, 2003), and the reviewed research shows that it also acts as a social glue between dogs and humans. Dogs synchronize their behaviors with that of humans in a variety of situations, and the degree of behavioral synchronization is dependent upon the degree of affiliation between the interacting partners. As is the case between humans, the more closely a dog is affiliated with a human, the more behavioral synchronization it will display. In addition, dogs exhibit social preferences for those people who synchronize with them.

How can we explain that dogs possess and exhibit such a human-like ability? Explaining the presence of a behavior in a species can be done through Tinbergen's inquiries.

First, we develop the ultimate causes of the behavior. From a *functional perspective*, dogs benefits by synchronizing their behaviors with that of humans, as it creates increased affiliation, potentially leading to more prosociality from the humans (i.e., several types of care) that could increase dogs' survival and fitness (Duranton, 2017, Chapter 6). Such suggestion is consistent with data comparing fitness and survival of offspring between pet dogs and other dogs' populations, which is higher in the first one compared to the latter (see Duranton, 2017, Chapter 6). We thus encourage investigating behavioral

synchronization between humans and other populations of dogs to increase the current knowledge of the advantages of behavioral synchronization for dogs. From a *phylogenetic perspective*, Hare and colleagues (Hare, Brown, Williamson, & Tomasello, 2002; Hare et al., 2005) put forward the domesticated cognition hypothesis. According to this hypothesis, humans and dogs underwent similar selective pressures for social skills and affiliation, leading to convergent skills for communication in both species (Hare, 2017). Behavioral synchronization (with conspecifics as well as with humans) should be studied in other domesticated mammals living in a human environment, such as cats, as well as in other canids, either nondirectly (e.g., foxes) or directly (e.g., wolves) related to dogs. Studies are also needed to investigate whether this social skill evolved early in dog domestication, prior to active artificial selection by humans, or whether it is associated with breed selection (see, for example, MacLean, Herrmann, Suchindra, & Hare, 2017). The present research partially answers this question, as we investigated behavioral synchronization in two different breeds. We found that dogs' interactions and sensitivity to humans' social cues, specifically when those humans are unfamiliar, are clearly affected by breed, and may therefore have evolved during modern artificial selection (Duranton et al., 2016, 2018c). However, when we looked at behavioral synchronization between affiliated partners, we found that pet dogs exhibited a high level of behavioral synchronization, whichever breed was tested (e.g., Duranton et al., 2017c), and it may therefore have evolved during early domestication (i.e., before modern artificial selection). Such an hypotheses would be consistent with the fact that no effect of sex was either found on dogs' behavioral synchronization with humans (Duranton et al., 2017a, 2018a, 2018b, 2018c), suggesting that this social skill might have been broadly selected through early domestication in all dogs. It is likely that ability to synchronize with humans, and sensitivity to human's behavioral synchronization, are two skills that have been selected for at different times in dogs' evolutionary history. The first one early on in domestication, as it is adaptive and found in all dogs, and the second with latter artificial selection linked to a specific breed's abilities. Finally, only breeds that had been selected to be attuned to their owners have been tested. Behavioral synchronization therefore needs to be investigated among other groups of breeds, selected for other tasks (i.e., hunting breeds) or solely for physical criteria (i.e., companion breeds).

Second, the proximal causes of the behavior. From an *ontogenic perspective*, behaviors are known to be the result of interactions between heredity and development (Gottlieb, 2002). When considering the ontogeny of dogs' social skills with regard to humans, which include behavioral synchronization, similarities between the socialization processes of humans and pet dogs could explain the similarities in social skills observed in these species. As both pet dogs and children develop in a human environment, they have similar learning opportunities that result in common behavioral social patterns across species (MacLean et al., 2017). This leads us to the two-stage hypothesis (Udell, Dorey, & Wynne, 2010, 2012; Udell & Wynne, 2010; Wynne 2016; Wynne, Udell, & Lord, 2008). This hypothesis suggests that ontogeny has a major impact on dogs' social cognition regarding humans (e.g. Udell et al., 2010; Wynne et al., 2008). The two stages are essential for a species to acquire sensitivity to humans' communicative signals. Stage 1 consists in socialization with humans during early development that allows dogs to regard humans as social companions, while Stage 2 consists in life experiences that allow dogs to flexibly learn the body movements of human companions that can be of importance, depending on their environment (Udell et al. 2010). The present research yielded data consistent with this hypothesis. Dogs from different subpopulations (and with different levels of interaction with humans) exhibit differing degrees of behavioral synchronization with humans (Duranton et al., 2017b, 2018b). The role of ontogeny is confirmed by the fact that older pet dogs are quicker to spontaneously switch actions after their owners have switched (temporal synchrony; Duranton et al., 2017a). To better understand the ontogeny of interspecific behavioral synchronization, investigating the existence and modalities of behavioral synchronization in various populations of canids (e.g., puppies, free-ranging dogs, wolves socialized with humans, wolf pups, foxes socialized with humans) is relevant.

However, even if the research area of dog–human behavioral synchronization is very promising, there is still a lot to be studied. Particularly, the fourth inquiry of Tinbergen, explaining a behavior from the *mechanistic perspective* (i.e., focusing on the mechanisms underlying the phenomenon) do need to be further investigated. Various behavioral mechanisms could be at play that would explain the dog behavioral synchronization described in the present review. In daily life, owners control access to the dogs' leash, leisure time, activities, and food. The owners choose the timing, direction, and duration of walks. They also choose the time and place where the dog encounters other dogs, humans, and so forth. The fact that the owner is mainly making decisions, such as initiating new directions of walks, may be considered as a type of leadership (Duranton et al., 2017a). Additionally, leaders are often individuals possessing special skills about, for instance, the environment, which is the case of humans over dogs in our societies (Ákos, Beck, Nagy, Vicsek, & Kubinyi, 2014). Another, probably more likely, mechanism for behavioral synchronization between dogs and humans is that dogs are reinforced for following their owners under many different circumstances. When a dog is on-leash, often the owner tugs on the leash whenever the dog pulls away, creating painful sensations that disappear only when the dog follows the owner: This is negative reinforcement for synchronizing the dog's movements with those of the owner (Gaunet & Deldalle,

2014). Whether dogs are on-leash or off-leash, many owners pet their dogs or give them treats for following them, or for coming back when called: This is positive reinforcement for synchronizing their movements with those of their owners (Duranton et al., 2017a). All of these phenomena may contribute to fostering the dog–human relationship and to making it beneficial for dogs to synchronize their movements (location, direction, walking speed) with those of their owner. Furthermore, as in humans, not moving in synchrony may be too costly for the dyad (e.g., decrease of cohesion and communication; Oullier & Scott Kelso, 2009), or at least not being synchronized with their owners may be too costly for the dogs (with, e.g., receiving punishment; Duranton et al., 2017). Effect of learning through life experiences is also confirmed by the findings that the older the dogs, the greater temporal synchrony we observed when switching activities (Duranton et al., 2017a), as well by the effect of affiliation discussed above. This suggests that social cognition, learning, and affiliation are involved in the synchronization of dogs' behavior with that of the human. However, one could argue that the described studies only evidenced synchronization due to proximity seeking in the dogs. Proximity-seeking behaviors are behaviors aiming at keeping or regaining contact/proximity with an individual mainly during anxious reactions (Fallani, Prato Previde, & Valsecchi, 2007). As proximity seeking is linked to affiliation (Gácsi, Topál, Miklósi, Dóka, & Csányi, 2001; Topál, Miklósi, Csányi, & Dóka, 1998), it could also explain why a lower degree of behavioral synchronization has been observed in lower affiliated dog–human dyads. Even if all of the studies limited stress as much as possible in order to avoid anxious reaction of the dogs that could have led to proximity seeking, further studies are needed to disambiguate the two phenomenon, in both natural and artificial settings. Finally, studies on other mechanisms, such as physiological and neural mechanisms, are highly encouraged as nothing is known about such mechanisms when it comes to dog–human behavioral synchronization.

To conclude, it is proposed that behavioral synchronization has a genetic basis (maintained through evolution and domestication), but can be modulated by life experiences (i.e., effect of affiliation), including learning (e.g., positive reinforcement when synchronizing with their owners). There is still much to understand, notably concerning the mechanisms at play and the higher cognitive processes linked to behavioral synchronization at an interspecific level between dogs and humans. In humans, nonconscious behavioral synchronization is thought to be a prerequisite for empathy and prosociality (Asendorpf, Warkentin, & Baudonnière, 1996; Kirschner & Tomasello, 2010; Mogan, Fischer, & Bulbulia, 2017; Stupacher, Maes, Witte, & Wood, 2017; Valdesolo, Ouyang, & DeSteno, 2010; Xavier, Tilmont, & Bonnot, 2013), but is the same true for synchronization between dogs and humans? If dogs exhibit behavioral synchronization with us, will they also exhibit prosociality and empathy toward us? Bringing behavioral synchronization into the field would yield relevant information and add to our understanding. Prosociality toward familiar conspecifics has recently been highlighted in dogs (Quervel-Chaumette, Dale, Marshall-Pescini, & Range, 2016a), but studies have so far failed to observe prosociality towards humans (e.g., Marshall-Pescini, Dale, Quervel-Chaumette, & Range, 2016; Quervel-Chaumette, Mainix, Range, & Marshall-Pescini, 2016b). Observing dog–human interacting partners with a high level of behavioral synchronization (already observed) could shed new light on this issue, as the latter may interfere with prosociality. This is a very promising line of research, especially given the importance of dogs as a biological model for understanding humans' social behaviors (see, for example, Bunford, Andics, Kis, Miklósi, & Gácsi, 2017).

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