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OUTLOOK

A new approach to understanding canine social cognition

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Summary
Domestic dogs have become well known for their socio-cognitive successes, so what does it mean when domestic dogs fail to cooperate? A new study by Marshall-Pescini, Schwarz, Kostelnik, Virányi, and Range (*PNAS, 114*(44) 11793–11798, 2017) highlights the importance of considering socioecological context, learning, and relationship quality when evaluating the social cognition of dogs and wolves.

Keywords Dog · Wolf · Cognition · Cooperation · Behavioral ecology

A large and growing body of research exists on the social behavior of canines, with a substantial focus on similarities and differences between domestic dogs and wolves. For many years, dogs were credited with outperforming wolves on a variety of tasks that required cooperation or responsiveness to human social cues. Early reports of dogs' successes at following human points and gaze to distant locations, coupled with poor performance by wolves, set the stage for the domestication hypothesis, which proposed that domestication had resulted in tame behavior and human-like socio-cognitive abilities in dogs. However, several decades later, our understanding of canine cognition has evolved substantially. Repeated demonstrations that human-socialized wolves are capable of succeeding on human guided tasks under equivalent testing conditions, and that the performance of dogs varies greatly by population, breed, age, morphology, and training history, has led to new questions with a greater emphasis on the unique lifetime and evolutionary variables that contribute to canine social cognition. This has resulted in new approaches with an eye toward the behavioral ecology of different canine populations and, consequently, a more balanced perspective of the socio-cognitive capacities of dogs and wolves. An important example comes from a recent paper published in *PNAS* by Marshall-Pescini, Schwarz, Kostelnik, Virányi, and Range (2017). In their study, wolves consistently outperformed domestic dogs on a series of cooperative string-pulling tasks where canines had to coordinate their actions with a familiar conspecific partner to succeed. These findings challenge earlier predictions that domestic dogs should be more skilled at cooperative tasks as a result of domestication.

In the first phase of their study, naïve dog dyads and wolf dyads were presented with a string-pulling apparatus without any prior training. Each dyad was given 2 minutes to solve the task, which required that both animals pull a rope simultaneously to reach a tray containing meat. Pulling on one rope independently resulted in it slipping out of the track, rendering the problem unsolvable. Each dyad experienced up to 48 trials over eight sessions. In this spontaneous condition, five out of the seven wolf dyads were successful at least once, with an average success rate of between 3% and 56%. Conversely, just one of the eight dog dyads were successful, and only on a single trial. A subset of these dog and wolf subjects were then provided with individual training where each animal was given the opportunity to concurrently pull two closely placed ropes on their own to reach the tray holding meat. Both dogs and wolves were able acquire this skill. After this training, they were again tested with conspecific partners for their ability to coordinate the action of pulling two widely spaced ropes simultaneously. Again, wolves outperformed dogs, with three out of four wolf dyads succeeding on the task at least once with a 14% to 92% success rate. Only two of the six dog dyads were successful on a single trial, achieving a 3% success rate. The authors of this study noted that both dogs and wolves appeared equally motivated to solve the task. No significant species differences in approach latency, time spent in proximity of the apparatus, or time spent looking at their conspecific partners were noted. Instead, the primary differences reported were that wolf dyads were (1) much more likely to

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simultaneously manipulate the apparatus, continuing to paw, bite, scratch and generally persist at the task when the other individual was present, and (2) wolves were more successful in solving the cooperative task.

The authors suggest that this outcome may be related to differences in the socioecology of wolves, which relies heavily on coordinated interactions with conspecifics, compared with that of domestic dogs, which show much greater variability in their dependence on conspecific cooperation. While Marshall-Pescini et al. (2017) suggest that higher rates of successful cooperative behavior among wolves represents divergence between the two species, they were also careful to identify contextual factors that might have further contributed to the observed outcomes. In doing so, their paper provides a platform for discussion about the variable nature of canine social cognition that takes into account learning, environment, and the behavioral ecology of different species and populations. For example, dogs and wolves from their study were raised in captive packs with minimal human interference. In this environment wolves established stable relationships, whereas dogs demonstrated more signs of conflict and less social stability. Given that closer social relationships predicted greater cooperative success in wolves, the absence of stable social relationships among the dogs may have influenced their performance independent of cognitive ability. In fact, an earlier study (Ostojić & Clayton, 2014) on cooperative string pulling found that pet dogs living in the same household were able to succeed on a similar task. As Marshall-Pescini and colleagues note, this difference is likely explained by the presence of more stable social relationships among pet dogs in human households, due to increased training and greater human management. Under conditions where dog–dog social relationships are less stable, behavioral strategies focused on avoiding conflict may take precedence over cooperative activity.

These findings are a reminder that identical rearing or testing conditions may not guarantee equivalent task performance, even if both species or populations share the capacity for a specific behavior or cognitive ability. Therefore, it is important that comparative social cognition studies evaluate whether each population was reared and tested under conditions expected to facilitate equivalent relationships among social partners before drawing conclusions about the cognitive ability of a species or group. This is not to imply that population or species differences do not exist; instead, a detailed understanding of the conditions that produce similar versus different comparative outcomes provides critical information about the mechanisms responsible for points of divergence. Given the hypothesized importance of social plasticity to the domestic dogs' success in diverse environments, this may be an especially relevant consideration in the field of canine cognition.

Another interesting aspect of Marshall-Pescini et al. (2017) is the finding that both dogs and wolves spent equivalent amounts of time looking toward their canine partner. However, for dogs, social referencing did not facilitate cooperative action or problem-solving success. This disconnect is significant because dogs' tendency to gaze at humans for extended periods of time during cognitive tests has often been used as a proxy for their cooperative nature or as evidence of human-like socio-cognitive abilities (Miklósi et al., 2003). Indeed, across a wide range of problem-solving contexts, dogs have been reported to spend significantly longer durations of time gazing at and seeking the proximity of humans compared with wolves (Miklósi et al., 2003; vonHoldt et al., 2017), and recent genetic evidence suggests that this difference could be linked to domestication (vonHoldt et al., 2017). However, gaze behavior in dogs often appears to be less discriminate and goal oriented than gaze behavior in wolves. For example, wolves have shown a stronger social bias toward familiar individuals, especially under conditions of social reciprocation or cooperative activity. While dogs also tend to prefer familiar attentive individuals, they spend significantly more time than wolves seeking the proximity of unfamiliar individuals, inattentive individuals and often exhibit prolonged gaze toward humans even when doing so results in decreased task success (vonHoldt et al., 2017). This would suggest that gaze is not always cooperative in nature and, as suggested by Marshall-Pescini and colleagues, may not always indicate prosocial intent.

The idea that dogs acquired greater cooperative skills, tameness, or a set of unique human-like socio-cognitive abilities during domestication that account for their success on a wide range of social tasks is appealing in its simplicity. However, as Marshall-Pescini et al. (2017) and others have pointed out, this perspective is likely oversimplified. Diving deeper into the origins of cognitive similarities and differences, including diverse socioecological pressures, lifetime experience, and the quality of social relationship exhibited by the individuals under test is an important step that promises to provide an even richer understanding of canine cognition going forward.

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