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The correlated evolution of social competence and social cognition

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Abstract

1. Knowing which of correlated traits are more strongly targeted by selection is crucial to understand the evolutionary process. For example, it could help in understanding how behavioural and cognitive adaptations to social living have evolved.
2. Social competence is the ability of animals to optimize their social behaviours according to the demands of their social environment. It is a behavioural performance trait that expresses how well a whole organism performs complex social tasks, such as choosing mates, raising offspring, participating in dominance hierarchies, solving conflicts or forming social bonds. Non-social competence, on the other hand, is the ability of animals to optimize their non-social behaviours according to the demands of their non-social environment, such as finding food or avoiding predators.
3. Social and non-social cognition are correlated lower-level traits of social and non-social competence, respectively, encompassing the underlying psychological and neural mechanisms of behaviour that allow animals to acquire, encode, store and recall information about their social and non-social environments.
4. Here, we employ the theoretical framework that selection acts on performance traits first and on lower-level traits only secondarily, to propose a new approach to the study of the evolution of social cognition.
5. We hypothesize that when selection favours social competence, the cognitive system becomes more adapted to the social domain, making species biased for social information, and increasing their degree of sociality. The opposite can happen when selection favours non-social competence.
6. The level of specialization that the cognitive system can attain depends on whether social and non-social competence are correlated with the same cognitive lower-level traits. This in turn will determine whether species will evolve a type of social cognition that is general—that contributes with cognitive abilities that can be used in both social and non-social environments—or modular—that contributes with cognitive abilities that are specific to the social environment.

KEYWORDS
environmental complexity, evolution, modular versus general intelligence, performance selection, social brain, social intelligence, social learning, whole-organism performance

1 | INTRODUCTION

One of the major questions in biology is to know which the main targets of selection are, namely understanding the relative importance of direct versus indirect selection on correlated traits (Irschick, Bailey, Schweitzer, Husak, & Meyers, 2007; Irschick, Meyers, Husak, & Galliard, 2008; Kingsolver et al., 2001). One hypothesis is that whole-organism performance traits—physical and behavioural capacities that express how well a whole organism performs an ecologically relevant task—are components of the phenotype that are more closely related to fitness than their correlated lower-level traits—the morphological, physiological, biochemical and cognitive mechanisms that underlie performance (Arnold, 1983; Garland & Losos, 1994; Irschick et al., 2007, 2008). What this implies is that selection should act more strongly on whole-organism performance traits and consequently that the evolution of lower-level traits should depend more on direct selection for performance traits than on direct selection for the lower-level traits themselves (Arnold, 1983; Garland & Losos, 1994; Irschick et al., 2007, 2008). In terms of a genetic response, this hypothesis suggests that versions of genes that enhance whole-organism performance lead to better survival and reproduction, which enables the individuals that carry these genes to pass them to their offspring along with the versions of genes for the lower-level traits that affected performance (Arnold, 1983; Garland, 1994; Garland & Losos, 1994). This paradigm might seem obvious, but when it comes to studying the physical and cognitive adaptations to the environment, researchers often use an oversimplified approach that selection acts directly upon these mechanisms, ignoring the 'crucial intermediate step of organismal performance' (Garland & Losos, 1994, p. 240). Here, we use this theoretical framework to reflect about the evolutionary process underlying cognitive adaptations to the environment, namely to social living.

Whole-organism performance traits can be divided into three components (Figure 1): (a) the maximum physical capacity of an animal, corresponding to its ability to perform a particular act in the best possible way, such as maximum sprint speed; (b) the behaviour that perfectly matches that capacity and that corresponds to the animal's maximum motivation, such as maximum sprint speed to escape a predator; and (c) the behaviour that the animal actually does when there are options available and that depends on its level of motivation, such as the decision to sprint less if the predator is still far away (Garland, 1994; Garland & Losos, 1994).

A lower-level trait correlated with whole-organism performance, namely with sprint speed, is the morphology of the animal's limbs, which imposes limits on its maximum physical capacity (Figure 1). If sprint speed is a more direct measure of fitness than limb morphology, selection should first act on maximum sprint capacity and only secondarily on how long or short the animal's limbs are. To test this hypothesis, Irschick et al. (2008) performed a comparative analysis of 20 studies that reported fitness measures regarding performance and morphological traits. They found no clear evidence for a stronger directional selection for performance than for morphology and suggested that the often strong inter-correlation between physical performance and morphology can equal the strength of selection between them (Irschick et al.,

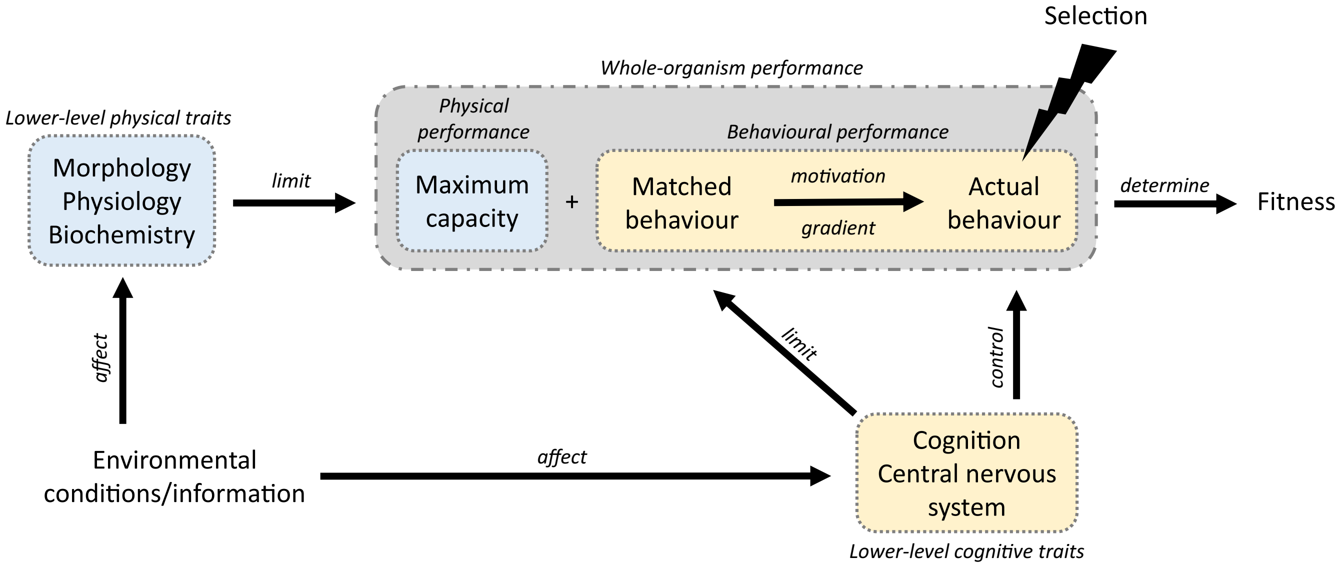

FIGURE 1 Paradigm of behavioural performance traits as direct targets of selection. The environment affects the phenotypic condition of animals, both physically and cognitively. Morphological, physiological, biochemical and cognitive traits will subsequently limit and control the whole-organism performance under those conditions. Whole-organism performance is the ability of animals to respond appropriately to environmental stimuli and can be divided into three types of traits: the animal's maximum physical capacity, the behaviour that matches perfectly to that capacity and the behaviour that the animal actually chooses to perform according to its motivational state. It is the whole-animal performance, and mainly the behaviour that the animal chooses to perform, that more directly determine the animal's fitness. Hence, selection is seen as acting most directly on decision-making behaviour, rather than on the other performance traits and even less on lower-level traits. Modified from Arnold (1983), Garland and Losos (1994) and Garland (1994)

2008). However, if a performance trait depends on the combined effects of various lower-level traits (e.g., limb morphology, and muscle physiology and biochemistry), the correlation between lower-level and performance traits is less perfect. In such cases, selection should still be weaker on each lower-level trait than on the performance trait itself (Arnold, 1983; Irschick et al., 2007; Irschick et al., 2008). Furthermore, if there are trade-offs between two performance traits (e.g., locomotor endurance may be more advantageous to escape from certain types of predators than sprint speed), performance for one of the traits may be under weaker selection against the other trait given that both cannot be optimized simultaneously (Garland, 1994; Garland & Losos, 1994; Irschick et al., 2007, 2008). This can even be more critical if different performance traits are correlated with the same lower-level traits, since they will be competing for the same resources. Therefore, when selection is stronger on one performance trait than in another, it should more strongly shape the adaptations of the lower-level traits to a specific function. In the above example, the species should either become specialized in sprint speed, hence favouring longer limbs with stronger muscles, or in locomotor endurance, favouring shorter limbs with more resistant muscles (for a more detailed discussion on the correlation between sprint speed and endurance, see Garland, 1994). This does not imply, however, that the animal completely loses its sprint speed or endurance abilities. It just means that it will become better at one of them.

Another set of lower-level traits correlated with whole-organism performance is the cognitive system, composed of the various psychological and neural mechanisms of information input, encoding, storage and retrieval (Figure 1). The cognitive system filters the information an animal obtains from the environment and determines how it responds to it. It, therefore, affects performance at the behavioural level by limiting what an animal can do, and controlling what it actually decides to do—the decision-making process—in face of its current motivation and environmental conditions. What this implies is that, similarly to the physical performance traits, the likelihood of making an appropriate or inappropriate decision in a given circumstance (e.g., deciding whether or not to sprint when a predator has been detected), as well as the trade-offs between concurrent behavioural decisions (e.g., deciding whether to start sprinting immediately or to delay the escape to continue feeding for a little longer), should also be more direct measures of fitness than the properties of each of the various mechanisms of the cognitive system responsible for processing that information. Besides, selection should act more directly on an animal's actual behaviour than on its maximum physical capacities (Garland, 1994; Garland & Losos, 1994). This is so because a behavioural decision can give the animal a performance advantage or disadvantage and, thereby, favour or compromise physical adaptations. A performance advantage would be, for example, the animal deciding to start sprinting away from the predator earlier than necessary because it has previously learned that its maximum speed is not too high, and a disadvantage would be the animal deciding to start sprinting later, because its maximum speed is high, although there is a risk that the predator will be better (Garland, 1994; Garland & Losos, 1994). The key role of behaviour as a filter between selection and physical performance has long been recognized (Garland, 1994; Garland & Losos, 1994; Lauder & Reilly, 1996). However, the correlation of behaviour with lower-level cognitive traits and how selection on behavioural performance affects the evolution of cognition has not yet been addressed.

Here, we propose a similar theoretical framework to study the correlated evolution of social competence and social cognition. If social competence is the 'ability of an animal to optimise the expression of its social behaviour as a function of the available social information' (Taborsky & Oliveira, 2012, p. 680), that is, the likelihood that the animal responds appropriately to the current circumstances, and social cognition the 'processes specific to knowing and acting on information about social companions' (Shettleworth, 2010, p. 415), that is, the decision-making process, then social competence can be seen as a behavioural performance trait and social cognition as a set of lower-level traits on which social competence depends. Our hypothesis is that selection shaped adaptations of the cognitive system to the social domain through its stronger effects on social competence than directly on cognition and through trade-offs of social competence with other behavioural performance traits. The latter we name 'non-social competence' and define as the ability of animals to respond appropriately to the current circumstances as a function of the available non-social information in the environment. This rationale has the following set of assumptions:

1. the social environment is a functional domain distinct from the non-social environment, which makes animals subjected to selection pressures in both domains, favouring the evolution of distinct behavioural performance traits, such as social and non-social competence;
2. social and non-social competence are evolutionarily correlated with lower-level cognitive traits, composed of mechanisms of information input, encoding, storage and retrieval;
3. the evolution of the lower-level cognitive traits is more strongly dependent on direct selection on social and non-social competence than on direct selection on the cognitive traits themselves;
4. there are energetic and temporal trade-offs that prevent social and non-social competence from being optimized simultaneously, which can be more critical if they share the same lower-level cognitive traits.

Based on these assumptions, two hypotheses can be proposed within this framework:

1. when selection is stronger on social than on non-social competence, the cognitive system becomes more adapted to the social domain, increasing the use of social information and, hence, species' degree of sociality;
2. the level of social specialization that the cognitive system can achieve depends on whether social and non-social competence are correlated with the same cognitive lower-level traits which

is determined by the type of trade-offs between performance traits.

These hypotheses generate the following predictions:

1. when temporal trade-offs are less costly than energetic trade-offs, performance traits tend to share the same lower-level cognitive traits and species will then evolve a type of general intelligence although more strongly shaped to the social domain (Figure 1a);
2. when temporal trade-offs are more costly than energetic trade-offs, performance traits tend to not share the same lower-level cognitive traits and species will then evolve a type of modular intelligence that can reach the highest levels of adaptation to the social domain (Figure 1b);
3. intermediate temporal and energetic trade-offs can favour the evolution of a type of mixed intelligence and, hence, with intermediate levels of adaptation to the social domain (Figure 1c).
4. similar cognitive adaptations to the non-social domain are expected if selection is stronger on non-social competence.
5. in none of these scenarios do stronger adaptations to one functional domain mean total loss of competences in the other functional domain.

In the following sections, we assess the rationale of our assumptions and hypotheses, reviewing in parallel the hypotheses that have historically been suggested to explain how the complexity of the social and non-social environments has shaped the evolution of cognition. Next, we demonstrate how our theoretical framework can generate predictions for the evolution of cognition that may explain the often puzzling patterns of general and modular intelligence found in past and current populations. We end by discussing how our ideas can be tested, describing the kind of data that would sustain our predictions, with examples that provide some preliminary evidence. We hope that our framework will help elucidating the long-lasting debate over whether social cognition is a special-purpose adaptation to social living or a general-purpose mechanism for the processing of both social and non-social information (e.g., Adolphs, 2009; Byrne & Bates, 2007; Heyes, 2012, 2016; Holekamp, 2006; Kendal et al., 2018; Rosati, 2017; Shettleworth, 2010).

2 | ASSESSING THE ASSUMPTIONS AND HYPOTHESES

2.1 | The evolution of social and non-social competence

While interacting with the environment, animals face varied types of biological information, some of which will affect their survival and reproduction (Wagner & Danchin, 2010). Part of that information is non-social information that animals acquire by directly interacting with the non-social abiotic (e.g., climate) and biotic (e.g., vegetation, parasites, predators and prey) variants that characterize their habitat (Taborsky & Oliveira, 2012; Wagner & Danchin, 2010). Direct interactions with the non-social environment allow animals to learn about their physical limitations in coping with different types of ecological conditions (e.g,. individual resistance to local parasites and diseases, or individual thermal tolerance boundaries), to learn about the location, availability and quality of resources (e.g., food and shelter), to acquire resource manipulation skills (e.g., from food handling or shelter construction), to improve predator avoidance and escape strategies and to develop individual preferences over available resource alternatives. This type of personal experience is highly valuable, as it generates throughout life, reliable, personalized, fitness-relevant information about ecological variants (Rieucau & Giraldeau, 2011; Wagner & Danchin, 2010). Moreover, non-social information can be quite complex, since the availability and quality of resources vary in space and time, as well as with the species home range size, activity period, substrate use, type of diet and predation pressure (Amodio et al., 2019; Holekamp, 2006; Powell, Isler, & Barton, 2017; Shettleworth, 2010). It is therefore expected that selection favours the evolution of adaptive, flexible behaviours that allow animals to cope appropriately with the different kinds of fitness-relevant information that they can extract from their non-social environment (Mikhalevich, Powell, & Logan, 2017). We call this set of adaptive behaviours ‘non-social competence’.

Another type of ecological variant that characterizes a species' habitat is social information, which animals obtain from interactions with, or observations of other social agents (Wagner & Danchin, 2010). Social agents are animals that share ecological requirements with each other, which usually occurs among conspecifics, but may also involve heterospecifics (Avarguès-Weber, Dawson, & Chittka, 2013; Wagner & Danchin, 2010). This implies that when social agents interact among each other or with their non-social environment, their behaviours provide fitness-relevant information to others (Avarguès-Weber et al., 2013; Danchin, Giraldeau, Valone, & Wagner, 2004; Rieucau & Giraldeau, 2011; Wagner & Danchin, 2010). This is so, because when assessing the quality of a resource, there are time and energy constraints that may limit individual choice optimization. However, the information provided by the choices and the performances of social agents could be quicker to acquire, safer and more accurate than individual assessment (Danchin et al., 2004).

With this kind of benefits, the frequency with which animals meet and interact with each other tends to increase, which may have led to the evolution of group living (Taborsky & Oliveira, 2012; Wagner & Danchin, 2003). In addition, if there are no strong selective pressures acting against group formation, such as scarce and non-shareable food sources or high predation risk, group living tends to persist and group sizes tend to grow (Danchin, Boulinier, & Massot, 1998; Varela, Danchin, & Wagner, 2007). Consequently, the number, duration and nature of the social interactions will also increase and diversify (Oliveira, 2013; Taborsky & Oliveira, 2012), making the social group a significantly different type of functional domain compared with the non-social environment (Adolphs, 2009; Byrne & Bates, 2007; Dunbar & Shultz, 2017; Oliveira, 2013; Taborsky & Oliveira, 2012). For example, animals in groups are members of dominance hierarchies (Bergman, Beehner, Cheney, & Seyfarth, 2003); they engage in complex mating interactions (Andersson & Simmons, 2006); they learn with each other how to identify and access the best resources (Thornton & McAuliffe, 2006); they can establish long-lasting social bonds (Dunbar & Shultz, 2007); they often provide parental care to their offspring and cooperate with conspecifics in raising each other's offspring (Covas, Plessis, & Doutrelant, 2008); they cooperate in many other contexts with both kin and non-kin (Rutte & Taborsky, 2007); and they may also engage in competitive, manipulative and deceptive interactions (Byrne & Bates, 2007). Moreover, the strategies employed for solitary foraging (Krebs, Erichsen, Webber, & Charnov, 1977) or predator avoidance (Caro, 2005) are different from those employed during group foraging (Giraldeau, Soos, & Beauchamp, 1994) or group defence (Caro, 2005), which generally involves specialized behaviours, such as cooperation and social coordination (Couzin, 2009; Sumpter, 2006).

The dynamics and information that social groups generate can, therefore, be very complex, since the feedback that animals receive from their social agents is highly diverse and variable over space and time, and will depend not only on the number of individuals in a group, but also on whether the same individuals repeatedly interact with each other, as well as on their characteristics, such as their identity, personality, age, size, social status and motivational states (Adolphs, 2009; Byrne & Bates, 2007; Dunbar & Shultz, 2017; Kappeler, 2019; Shettleworth, 2010; Taborsky & Oliveira, 2012). It is therefore expected that natural selection also favours the evolution of adaptive, flexible behaviours that allow animals to cope appropriately with the different kinds of fitness-relevant information that they can extract from their social environment, and even to capitalize on the opportunities provided by their social environment (Mikhalevich et al., 2017; Taborsky & Oliveira, 2012). This set of adaptive behaviours has been named 'social competence' (Taborsky & Oliveira, 2012).

It seems, therefore, evident that both the social and non-social environments are challenging, that animals during their lives must respond to the stimuli of both environments, and that selection consequently made the animals competent to use both types of information for decision-making. However, social and non-social competence may be difficult to optimize simultaneously because animals do not have unlimited time and energy to attend to all stimuli equally. Knowing additionally that the relative complexity of the social and non-social environments differs across space and time, different populations are likely to evolve dissimilar levels of social and non-social competence. If that is the case, the question we ask is how distinct selective pressures on social and non-social competence have secondarily shaped the evolution of cognition.

2.2 | The evolution of social and non-social cognition

Among the many hypotheses that have been suggested to explain the evolution of cognition (reviewed in Byrne & Bates, 2007; Dunbar & Shultz, 2017; Rosati, 2017), the social intelligence or social brain hypothesis posits that it is the complexity of social interactions, mainly those generated from semi-permanent, cohesive, bonded and functional social groups, that determine the evolution of enhanced cognitive abilities (Dunbar & Shultz, 2007, 2017). The ecological intelligence hypothesis, on the other hand, posits that enhanced cognition is achieved to meet the challenges of the non-social environment, namely the complexity associated with the manipulation and finding of temporally and spatially distributed food (Powell et al., 2017; Rosati, 2017). Similarly, the predator–prey intelligence hypothesis suggests that is the complexity of predator–prey interactions that has most contributed to the evolution of intelligence in both predators and prey (Amodio et al., 2019; Zuberbühler & Jenny, 2002).

These hypotheses, although competing, suggest a similar model of cognition evolution, namely that the complexity of social, ecological or predator–prey interactions have led to the evolution of many, diverse and enhanced cognitive abilities (Shettleworth, 2010). These are abilities that although evolved in one functional domain are advantageous in all domains, because it is assumed that the cognitive mechanism is general, that is, the sub-mechanisms of information input, encoding, storage and retrieval are shared between functional domains. The three hypotheses also predict the evolution of large executive brains, with increased processing and storage capacity. Because larger brains (relative brain size or neocortex size) are energetically expensive—using circa 20% of the total energy intake in humans (Aiello & Wheeler, 1995)—their adaptive significance is puzzling, unless if correlated with enhanced intelligence (Byrne & Bates, 2007; Dunbar & Shultz, 2007, 2017; Powell et al., 2017; Rosati, 2017).

A positive correlation between cognitive abilities and relative brain size has received support from studies with primates (Dunbar & Shultz, 2007; Street, Navarrete, Reader, & Laland, 2017; Zuberbühler & Jenny, 2002) and several other vertebrate groups (Fox, Muthukrishna, & , Shultz, S., 2017; Kotrschal, Corral-Lopez, Amcoff, & Kolm, 2015; Pérez-Barbería & Gordon, 2005; Sayol et al., 2016). However, some findings are contradictory, contentious or puzzling (Dunbar & Shultz, 2017; Holekamp, 2006; Powell et al., 2017; van der Bijl & Kolm, 2016), and complex social and non-social behaviour and cognition have also been found in small-brained animals such as bees, ants, wasps, fruit flies or even nematodes (reviewed in Chittka & Niven, 2009; Grüter & Leadbeater, 2014; Leadbeater & Dawson, 2017). For insects, in particular, no positive correlation between relative brain size and degree of sociality—a proxy of cognitive abilities—has been found, with selection favouring more specialized neural circuits rather than bigger brains (Lihoreau, Latty, & Chittka, 2012). Large brains have, therefore, been claimed to not convey a good association with enhanced cognitive abilities, at least as long as we do not understand more about brain functioning (Chittka & Niven, 2009; Dunbar & Shultz, 2017; Healy & Rowe, 2007; Rosati, 2017).

A different approach has been to ask whether social, ecological and predator–prey intelligence, instead of relying on a unique type of cognition—the general-purpose brain—rely on special-purpose cognitive modules, which can be highly specialized and do not necessarily need to correlate with enlarged brain sizes (Chittka & Niven, 2009). Each special-purpose cognitive module, with its independent mechanisms of information input, encoding, storage and retrieval, would correspond to one or several distinct cognitive abilities, allowing animals to use different information in truly different ways (Rosati, 2017). At the level of brain evolution, these special-purpose mechanisms would have to be found either on specific brain parts, brain structures or neural networks (Chittka & Niven, 2009; Kendal et al., 2018; Oliveira, 2013). This is the modularity hypothesis of cognition evolution (Adolphs, 2009; Byrne & Bates, 2007; Chittka & Niven, 2009; Rosati, 2017; Shettleworth, 2010).

Social learning, for example, one of the best known and most studied social cognitive mechanisms, is in the centre of this debate (Heyes, 2012, 2016; Kendal et al., 2018; Leadbeater & Dawson, 2017; Lefebvre & Giraldeau, 1996; Lotem & Halpern, 2012). Because it generates knowledge specifically about the social environment, it has been considered a special-purpose mechanism distinct from asocial learning (see discussions in Kendal et al., 2018; Leadbeater & Dawson, 2017; Lefebvre & Giraldeau, 1996; Lotem & Halpern, 2012). However, since social and asocial learning seem to employ similar associative learning rules, other authors argue that they constitute one single, general-purpose cognitive mechanism (Heyes, 2012, 2016).

Comparative studies have been more supportive of a general learning mechanism, conserved across species, than of adaptive, independent, specializations for social and asocial learning. This is so, because social learning correlates positively with asocial learning both across species and across individuals within species (Heyes, 2012; Reader & Laland, 2002) and occurs in solitary animals (Heyes, 2012; Webster & Laland, 2017). However, this comparative approach has been criticized, because correlations do not prove causality and the quantitative genetics underlying social behaviours, including social learning, differs from behaviours that do not vary with the social environment in which they are expressed (Bleakley, Wolf, & Moore, 2010). Moreover, species contrast in their behavioural ecologies, which may impair their performance in social learning tasks in the laboratory (Lefebvre & Giraldeau, 1996; Templeton, Kamil, & Balda, 1999). Thereby, only within- versus between-species comparisons should allow to correctly determine whether the performance of a given species is enhanced or not in a social learning task (Lefebvre & Giraldeau, 1996).

To our knowledge, only Templeton et al. (1999) conducted one of these studies and found that pinyon jays *Gymnorhinus cyanocephalus*, a corvid species who lives in large colonies of up to hundreds of individuals, had better performance at a social than an asocial learning task, while Clark's nutcrackers *Nucifraga columbiana*, another corvid species with similar foraging ecologies and habitat requirements, but who lives in family groups of two to four individuals, performed equally well on both tasks. Such differences can indeed be explained by adaptations of the learning mechanism to social and non-social information, but other explanations are nevertheless possible. According to Heyes (2012, 2016), when species perform better in social than in asocial learning tasks it should not be because the learning mechanism is adaptively specialized, but because the species' sensory system is biased towards social information.

This debate about whether the cognitive system is general or modular is unlikely to reach consensus for two reasons. First, because fundamental knowledge about brain functioning is still lacking, and second because the social, ecological and predator-prey hypotheses of cognition evolution do not clearly distinguish which of correlated traits should be more directly targeted by selection—if behavioural performance traits or cognitive traits. According to these hypotheses, selection favours individuals that perform well in the social, ecological or predator–prey functional domains and that simultaneously possess enhanced general or modular cognitive systems, as well as larger brains. Here, researchers predetermine which relationships between behavioural performance and cognition should occur. With our conceptual approach, we place the emphasis on behavioural performance traits as the direct targets of selection (Arnold, 1983; Garland, 1994; Garland & Losos, 1994; Irschick et al., 2007, 2008), which we think will help clarifying the debate. Our proposal is that behavioural performance traits are evolutionarily correlated with lower-level cognitive traits and that selection should first favour individuals that perform well in a given functional domain (social or non-social) and only secondarily the type of cognition (modular or general) and brain size (large or small) that they happen to have. No predetermined relationships between traits are assumed. This allows to hypothesize that selective pressures favouring different performance traits shape the cognitive system differently. For example, when group living is especially advantageous, and the social environment becomes progressively more complex, selection should be stronger on social competence than on non-social competence and, by doing so, indirectly select for the type of cognition and brain size that better process social information. Similarly, when the non-social environment becomes progressively more complex, selection should favour non-social competence and hence contribute to the non-social specialization of the cognitive system.

Our approach agrees with other theoretical and conceptual frameworks for the evolution of cognition, which predict that environmental complexity promotes behavioural flexibility and enhanced cognitive capacities (Mikhalevich et al., 2017), and that the cognitive system becomes specialized, with only relevant data being acquired and the cognitive mechanism only incorporating the data patterns that are useful (Lotem & Halpern, 2012). What our approach further clarifies is that cognition evolves by indirect selection and that the degree to which the cognitive system can become specialized depends on whether social and non-social competence are evolutionarily correlated with the same lower-level cognitive traits and that this is determined by the type of trade-offs between performance traits. Thus, our approach generates predictions about whether the cognitive system is general or modular. In the next section, we will develop these predictions with some illustrative examples focusing our argument on the evolution of social cognition.

3 | THE SOCIAL SPECIALIZATION OF THE COGNITIVE SYSTEM

3.1 | Scenarios of correlated evolution between social competence and social cognition

Following our approach that cognition evolves indirectly through selection on behavioural performance traits, we predict that when performance traits share the same lower-level cognitive traits, species should develop a type of enhanced general intelligence. This happens, because the same cognitive system is used to respond to all types of stimuli, social and non-social. In such cases, when selection is stronger on social competence, we additionally predict that the general cognitive system can become specialized to the social domain through the emergence of cognitive abilities especially adapted for social decision-making. This could be the case, for example, of transitive inference, a cognitive ability that allows animals to recognize dominance hierarchies but that can be useful outside the social domain (MacLean, Merritt, & Brannon, 2008; Tibbetts, Agudelo, Pandit, & Riojas, 2019). Animals in this circumstance develop an enhanced cognitive system that although general is also predominantly social (Figure 2a). This scenario of cognition evolution may explain the puzzling results of comparative studies that in some species better associate enhanced general intelligence with complex social living and in others with complex ecological or predator–prey effects (van der Bijl & Kolm, 2016; Dunbar & Shultz, 2017; Holekamp, 2006; Powell et al., 2017). These species, although apparently similar because of their general cognitive mechanisms, differ in their past selective pressures, which is a difference that should be able to be observed at two levels: they should be characterized by a different set of cognitive abilities (e.g., transitive inference should not be present in species whose past selective pressures did not favour social competence) and should be able to use their abilities equally well in all functional domains (e.g., social species should be equally good at transitive inference tasks, whether with social or non-social information).

This scenario of enhanced general intelligence generates, however, temporal trade-offs between the processing of social and non-social information, since both have to time share the same lower-level cognitive traits. Attention, for example, could become a key limiting factor for the information that animals can extract simultaneously from the environment. When that is the case, independent, specialized, input mechanisms for the detection of different types of information should be more advantageous than one general input mechanism. We, therefore, predict that under temporal trade-offs and selective pressures that favour social competence, the cognitive system can further become specialized to the social domain by the emergence of a social input mechanism that is predominant over the others. Animals in this circumstance develop a type of mixed intelligence biased towards the social domain (Figure 2c). Consequently, animals will tend to solve tasks in any functional domain mainly with social information and together with their social companions. For example, animals should tend to learn where to find food or how to detect predators mainly from paying attention to the behaviours of other social agents than from paying attention directly to the non-social information (Galef & Wigmore, 1983; Thornton & McAuliffe, 2006). This prediction was made by Dunbar and Shultz (2007) in the context of the social intelligence hypothesis, but it is valid for the ecological and predator–prey hypotheses as well. This could also explain why, as predicted by Heyes (2012), better performances in social than asocial learning in some species could result from specializations of the input mechanism alone and not from specializations of the actual learning mechanism. If that is the case, we can further predict that social species should perform equally well in learning tasks when social and asocial stimuli are presented separately, but learn better with social stimuli when they are presented simultaneously.

However, the scenario of enhanced mixed intelligence can still generate temporal trade-offs between the remaining lower-level traits. If such trade-offs are very costly, we predict that more, if not all lower-level traits should stop being shared between performance traits. This allows: (a) more flexible responses, with animals processing different information through distinct mechanisms; and (b) parallel processing, with faster responses to stimuli that are presented simultaneously. Animals in this circumstance develop a type of modular intelligence (Figure 2b), which is in agreement with the modularity hypothesis of cognition evolution (Adolphs, 2009; Byrne & Bates, 2007; Chittka & Niven, 2009; Rosati, 2017; Shettleworth, 2010). This implies that cognitive traits specialized to process social or non-social information can evolve independently under distinct selective pressures. Moreover, one expects that if selection favours social competence, the social cognition module becomes more developed than the others, with social cognitive abilities reaching higher levels of complexity than non-social ones. This scenario of cognitive modularity could explain within- and between-species variations in cognitive abilities, given that enhanced cognition in the social domain does not necessarily correlate with enhanced cognition in the other domains, nor vice versa. Comparative studies across closely related lemurs show that social and non-social cognitive abilities are not general but can, instead, have different levels of complexity (Rosati, 2017). In species that are more social and folivorous, visual perspective taking, gaze following and transitive inference abilities are more developed, which are cognitive abilities more useful in the social domain. Whereas in species that are less social and are mainly frugivorous, lemurs have high spatial memory and motor inhibitory control abilities, which they need for finding and manipulating temporally and spatially distributed fruit patches (Rosati, 2017).

However, given the finite energy available for parallel brain activity, the evolution of independent cognitive modules may also raise energetic trade-offs between lower-level cognitive traits. We, therefore, predict, that in the case where energetic trade-offs are very costly, some cognitive traits could return to being shared between social and non-social competence, with the evolution of the whole cognitive system eventually reaching a parsimonious compromise of resource distribution between performance traits, finally generating a type of optimized mixed intelligence (Figure 1c). The evolutionary outcome of cognitive lower-level traits that remain shared and not shared should differ between species, depending on phylogenetic constraints and on the interplay between social and non-social selective pressures.

Munger et al. (2010) provide an enlightening example of a mixed cognitive system in mice *Mus musculus*. They studied how social olfactory cues are integrated by the mice olfactory nervous system, having identified specialized olfactory sensory neurons for carbon disulphide. Carbon disulphide is a component of rodents' breath,

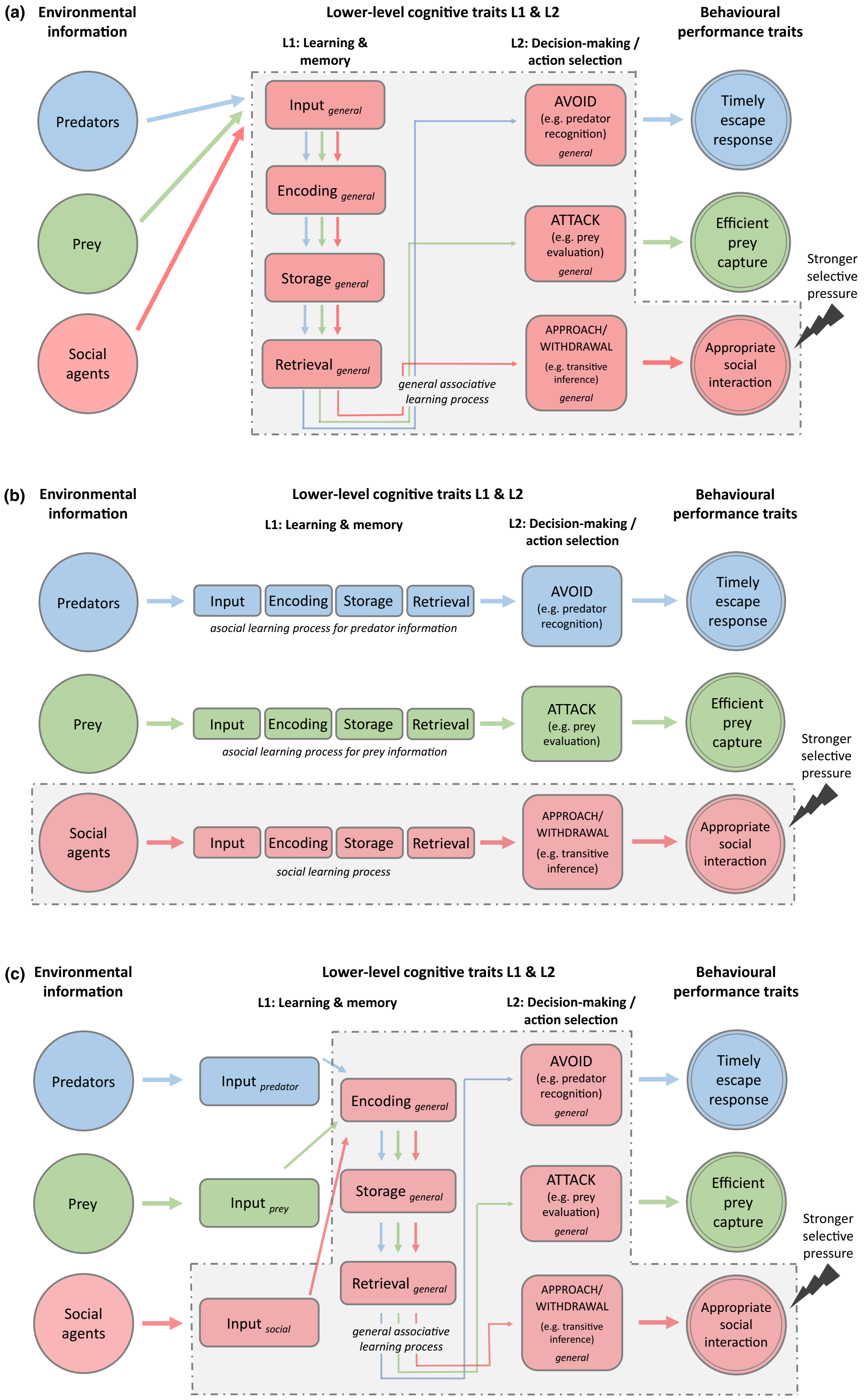
(a)
Environmental information
Lower-level cognitive traits L1 & L2
Behavioural performance traits
L1: Learning & memory
L2: Decision-making / action selection
Predators
Prey
Social agents
Input general
Encoding general
Storage general
Retrieval general
AVOID (e.g. predator recognition) general
ATTACK (e.g. prey evaluation) general
APPROACH/ WITHDRAWAL (e.g. transitive inference) general
general associative learning process
Timely escape response
Efficient prey capture
Appropriate social interaction
Stronger selective pressure
(b)
Environmental information
Lower-level cognitive traits L1 & L2
Behavioural performance traits
L1: Learning & memory
L2: Decision-making / action selection
Predators
Input
Encoding
Storage
Retrieval
asocial learning process for predator information
AVOID (e.g. predator recognition)
Timely escape response
Prey
Input
Encoding
Storage
Retrieval
asocial learning process for prey information
ATTACK (e.g. prey evaluation)
Efficient prey capture
Stronger selective pressure
Social agents
Input
Encoding
Storage
Retrieval
social learning process
APPROACH/ WITHDRAWAL (e.g. transitive inference)
Appropriate social interaction
(c)
Environmental information
Lower-level cognitive traits L1 & L2
Behavioural performance traits
L1: Learning & memory
L2: Decision-making / action selection
Predators
Prey
Social agents
Input predator
Input prey
Input social
Encoding general
Storage general
Retrieval general
general associative learning process
AVOID (e.g. predator recognition) general
ATTACK (e.g. prey evaluation) general
APPROACH/ WITHDRAWAL (e.g. transitive inference) general
Timely escape response
Efficient prey capture
Appropriate social interaction
Stronger selective pressure

FIGURE 2 Scenarios of correlated evolution between social competence and social cognition. Both social and non-social environments produce different types of fitness-relevant information. For example, information about approaching predators, prey accessibility and dominance interactions between social agents. This information is processed by the cognitive system, which controls, through learning, memory and decision-making processes, the behavioural responses of the animals. The more appropriate the behavioural responses, the higher their behavioural performance. Performance traits can be social or non-social and be correlated with the same or different lower-level cognitive traits. (a) If all cognitive traits are shared between performance traits, species are considered to have a general intelligence, allowing them to respond to different information with the same cognitive abilities; (b) if cognitive traits are not shared between performance traits, species are considered to have a modular intelligence, allowing them to respond to different information in different ways; (c) if only some cognitive traits are shared between performance traits, species are considered to have a mixed intelligence. In all scenarios, when selection is stronger on social than on non-social competence, the cognitive system becomes more adapted to the social domain (shown in grey)

implicated in the social learning of conspecific food choices (Galef & Wigmore, 1983; Munger et al., 2010). Munger et al. (2010) identified (a) three types of carbon disulphide receptors, (b) specialized olfactory neurons expressing the three receptors and (c) a subset of atypical olfactory bulb targets—the necklace glomeruli—to which the olfactory neurons connect in the main olfactory system. The association between a food odour (detected by a distinct subpopulation of olfactory neurons) and the carbon disulphide happens at the level of the necklace glomeruli, where information from both food and carbon disulphide chemo-stimuli is integrated. Disruption of the carbon disulphide olfactory neurons prevents mice from acquiring social information and consequently from activating memory centres in the hippocampus to gain a socially transmitted food preference. This discrete neural circuit for carbon disulphide constitutes a specialized olfactory subsystem that mediates food-related social learning (Munger et al., 2010). This example provides an illustration of how selection for enhanced social competence—learning from conspecifics which foods are safe—may have shaped both the sensory system (with specialized sensory neurons for social information acquisition) and the encoding system (with specialized olfactory bulb targets where integration of stimuli occurs) to the social domain, while the information storage and retrieval mechanisms seem to have remained unspecialized. Social learning could, therefore, be a cognitive mechanism that uses both specialized and general neural circuits in the brain.

All three scenarios of cognitive evolution that we here suggest predict the specialization of the cognitive system to the social domain. However, we recall that specializations could be social or non-social, depending on the relative strength of selection on social and non-social competence and on the type of trade-offs between them.

3.2 | Measuring social cognition adaptations

For the cognitive system to achieve a degree of specialization to the social domain, species are expected to have evolved specific, diverse and enhanced cognitive abilities that would provide them with better tools for social decision-making. At the brain level and depending on each species evolutionary constraints and each scenario of correlated evolution between social competence and social cognition (Figure 2), these adaptations could be achieved with new, faster and/or more efficient neural networks for processing social information. This would have to involve higher neural circuitry specialization, greater replication of neural circuits or greater sensitivity to neuromodulators and steroid hormones. In particular for information input mechanisms, these adaptations could add precision and detail to sensory processes that would lead to more salient social information (Adolphs, 2009; Byrne & Bates, 2007; Chittka & Niven, 2009; Heyes, 2012, 2016; Lotem & Halpern, 2012; Oliveira, 2013). For example, Barton (1998) found that brain size variation in primates is associated with visual specialization: both the number and volume of cells of the parvocellular pathway, which is sensitive to wavelength, increase with larger social groups in diurnal primates. For information encoding, storage and retrieval mechanisms, these adaptations could add storage capacity, parallel processing and/or facilitate associations with social information (Leadbeater & Dawson, 2017; Lefebvre & Giraldeau, 1996; Lotem & Halpern, 2012), like the case of the specialized social learning system in mice that we described above (Munger et al., 2010). And in what concerns decision-making mechanisms, adaptations could be found in the reward system, adding more value to social information than to non-social information and, hence, making it a priority for the cognitive system, so that species will tend to use social information more often and to make decisions based on social information more frequently (Grüter & Leadbeater, 2014; Kendal et al., 2018; Oliveira, 2013; Rendell et al., 2011). Studies of dopaminergic neural circuits, which are implicated in the reward system of vertebrates and invertebrates, could help elucidating whether between closely related species the more social ones have, for example, greater sensitivity to dopamine, greater replication of dopaminergic circuits, or dopaminergic neurons reaching more areas of the brain and hence modulating a greater range of behaviours.

Lastly, at the behavioural level, cognitive and neural adaptations to the social domain could be detected by an increased repertoire of social behaviours and with increased flexibility (Chittka & Niven, 2009; Mikhalevich et al., 2017). This is valid for all three scenarios of correlated evolution between social competence and social cognition (Figure 2). However, when some degree of modularity is present, behavioural variability should be higher as social information is more differently processed from non-social information and hence truly different behavioural responses are produced (Rosati, 2017). Moreover, with enhanced cognition, behavioural performance should also improve and hence we could expect animals to increase their ability for deciding which behaviours are more appropriate to each situation.

Testing animals for decision-making in limiting situations, where they are expected to respond with maximum motivation, would be a way of finding variations in behavioural performance within and between species, including in selection studies. This incluses making decisions with social information in a greater range of situations, the so-called social learning strategies (Grüter & Leadbeater, 2014; Kendal et al., 2018; Rendell et al., 2011), such as copying conspecifics more frequently ('when' strategies), copying more different types of information ('what' strategies) and/or copying information from more individuals in the group ('who' strategies). We make this prediction, because when the social environment becomes more complex, there is more fitness-relevant information available at any one time, produced by each individual and/or by more individuals in the group (Mikhalevich et al., 2017). This should make social learning more advantageous and conversely asocial learning costlier, less durable or less reliable. Species that are more social should also be more prone to update or cumulate knowledge with new available social information. This strategy increases task knowledge and facilitates the spread of behavioural traditions, as studies with human children have shown (Wood, Kendal, & Flynn, 2013, 2015). Such increased use of social information can reinforce selective pressures on social learning performance, thereby affecting cognition again and further facilitating cultural dissemination (Dunbar & Shultz, 2017; van Schaik & Burkart, 2011; Street et al., 2017).

4 | CONCLUDING REMARKS

The evolution of social cognition has long been a subject of interest to researchers. Especially because human societies portray so well the complexity that the social environment can achieve, and human enhanced social competence, cognition and brain size are examples of putative adaptive responses to this kind of environment (Adolphs, 2009; Byrne & Bates, 2007; Dunbar & Shultz, 2007; Kendal et al., 2018; Tremblay, Sharika, & Platt, 2017). In nonhuman species, however, these positive correlations are not perfect (Chittka & Niven, 2009; Dunbar & Shultz, 2017; Healy & Rowe, 2007; Rosati, 2017), which makes it unclear how these adaptations evolved and how do they affect each other. Here, we propose the conceptual approach that the evolution of cognition is shaped by selective pressures on behavioural performance traits—social and non-social competence—and not the reverse. Hence, social cognition can evolve indirectly if selection favours social competence. This approach allows to predict that species exposed to different social and non-social selective pressures will evolve different behavioural performances and, secondarily, different cognitive systems, some more predominantly social than others. Such diversity also means different ways of interacting back with the environment and, hence, of exploring its resources, of constructing new niches, of establishing new cultures and thereby creating new selective pressures. We hope our proposal helps elucidating the debate on cognition evolution, namely that of social cognition, and encourages the design of future studies.

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AUTHORS' CONTRIBUTIONS

All authors planned the overall layout of this review paper together. S.A.M.V. and M.C.T. wrote first drafts of specific sections in close collaboration with R.F.O. All authors reviewed the final text.

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