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First predict, then bond: Rethinking the function of mimicry from prediction to affiliation in human and non-human animals

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ABSTRACT

Automatic mimicry, where social animals mimic the emotional expressions of others, is a well-documented phenomenon. While research has extensively examined how being mimicked influences our perception of others, the fundamental question of *why* we mimic remains largely unexplored. Previous theories often link mimicry with an affiliative social goal. While we agree that mimicry can increase survival chances by enhancing group cohesion, we argue for a more primitive adaptive value that may operate independently of social bonding. By reviewing existing literature, we propose that mimicry serves as a mechanism to predict other individuals, and consequently, the environment, enhancing survival of the individual. We posit a shift towards understanding mimicry as a mechanism that minimizes prediction error, empowering individuals to navigate their surroundings more effectively. Embracing mimicry as a tool for self-preservation and environmental prediction opens new avenues for interdisciplinary research in comparative psychology and behavioral ecology.

Social animals frequently display automatic mimicry, wherein an expression of an observed other triggers an unconscious similar expression in the observer (Prochazkova and Kret, 2017). While research has focused on the possible moderators of mimicry and, to a lesser extent, the consequences of being mimicked (Hale and Hamilton, 2016a) the fundamental question of *why* we mimic remains one of the most complex, unanswered questions in psychology. Mimicry is a multifaceted phenomenon, and its emergence over the course of evolution has likely been shaped by a combination of ultimate causes. Several theories have attempted to explain mimicry's function, offering diverse perspectives on its evolutionary origins, from facilitating social learning and coordination to functioning as a social bonding mechanism. Some researchers suggest that mimicry evolved primarily for learning and coordination, emphasizing the cognitive and motor benefits of imitating others (Chartrand and Bargh, 1999). Others propose that, while mimicry may have originated as a learning mechanism, it has several benefits in the here and now, that is, mimicry may act as a "social glue" enhancing group cohesion (Lakin et al., 2003), and regulating social interactions, therewith increasing affiliation (Fischer et al., 2012). Yet there are other sounds as well. For example, Wang and Hamilton (2012) ascribe a more strategic functionality to mimicry. These authors posit mimicry as a Machiavellian tool for advancing social standing, suggesting a calculated use in navigating complex social hierarchies (Wang and Hamilton, 2012). Despite their nuanced differences, these theories converge on a common theme: linking mimicry to an affiliative context, predetermined social goal, and general positive social consequences (e.g., group cohesion, liking).

Undoubtedly, affiliating with others offers numerous advantages crucial for survival, such as protection from predators and increased access to resources that enhance fitness (Micheletta et al., 2012; Silk et al., 2003). These direct adaptive advantages likely exerted significant selective pressure on the evolution of mimicry. However, the affiliative results often associated with mimicry may also reflect emergent properties – consequences that arise from the collective effects of mimicry – rather than the driving force behind its evolution. In other words, while mimicry can foster social bonding, this outcome may be a beneficial side effect of a behavior originally selected for other purposes. In this perspective paper, we build on previous theories to disentangle the function of mimicry – its ultimate evolutionary purpose and adaptive significance for the individual – from its emergent properties, the observable results in the social environment, or the changes in the group dynamics. While acknowledging the importance of affiliation in the

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context of mimicry, we propose that a more comprehensive understanding of this phenomenon must consider its primary functions for the individual that mimics. Our argument centers on the notion that emotional expressions, which are often the subject of mimicry, serve crucial adaptive purposes for the expressor. For instance, the facial configuration associated with disgust, characterized by a wrinkled nose and raised upper lip, functions to restrict the nasal passages and limit the intake of potentially harmful substances (Curtis et al., 2011). Similarly, the widened eyes typical of a fearful expression increase the visual field and enhance the perception of potential threats in the environment (Susskind et al., 2008). These expressions may also result in others who perceive them looking around to figure out what is wrong and that may be advantageous for both expressor and perceiver. However, that is a side-effect and not the primary reason why the expression - in this specific configuration of the facial muscles - was useful in the first place. When we mimic these expressions from nearby conspecifics, we may gain similar direct benefits: by mimicking a disgusted expression, one might preventively protect against ingesting noxious materials. Similarly, mimicking a fearful expression could lead to increased vigilance and threat detection. Moreover, mimicking these expressions may foster a shared perceptual experience among individuals, making it easier to coordinate and conquer the threat together. Our idea is that engaging in mimicry may result in increased overlap between individuals, making the other – and consequently the surrounding environment – easier to predict. We will begin by defining automatic mimicry (**Section 1**), and then review the literature supporting the theory that mimicry serves an affiliative and social regulatory function (**Section 2**). Following this, we will explore the literature presenting findings that challenge the affiliative account of mimicry (**Section 3**), offering evidence that this viewpoint does not fully explain the entire body of research on mimicry and may oversimplify the phenomenon. We will propose that a potential ultimate cause of mimicry might be to facilitate the prediction of the environment and the behavior of conspecifics with direct benefits for the self (**Section 4**). In the final section, we will propose some guidelines for testing this alternative hypothesis (**Section 5**). The growing interest and evidence for predictive coding as a unifying principle of brain function aligns with the potential for mimicry to facilitate the prediction of the environment and behavior of others. Reevaluating mimicry through this lens could yield new insights. More broadly, psychology is shifting towards more rigorous, mechanistic accounts of psychological phenomena. Clarifying the fundamental purpose of this ubiquitous social phenomenon could have wide-ranging implications for our understanding of social intelligence and adaptation. Finally, with the now widespread use of mimicry in human-AI interaction (Devillers, 2021), understanding the theoretical underpinnings of mimicry in humans and non-human animals has become more urgent.

1. What is automatic mimicry?

Automatic mimicry is traditionally defined as the unconscious and spontaneous imitation of other people's behaviors, gestures, and expressions without deliberate intention or awareness (Chartrand and van Baaren, 2009). However, there is a considerable debate surrounding what is mimicry versus other forms of alignment (e.g., synchrony, true imitation, emotional contagion, etc.), with certain nuances presenting gray areas for discussion. Before we delve further into the explanation, it is imperative to establish the definition of automatic mimicry that we intend to use. We derive the definition from Prochazkova and Kret (2017), where the authors use 'automatic mimicry' – from now on referred to as mimicry – as an umbrella term for different types of synchronous behaviors that occur at multiple levels without awareness (Prochazkova and Kret, 2017). The authors distinguish between motor mimicry (involving muscle movements) and autonomic mimicry (physiological changes). Motor mimicry happens when two or more people engage in mimicked motor movements such as facial expressions (Likowski et al., 2012), body posture (Tia et al., 2011), gestures that accompany speech (Kimbara, 2006), vocal features (Smith-Genthôs et al., 2015), laughter (Davila-Ross and Palagi, 2022), yawning (Massen and Gallup, 2017), and scratching (Schut et al., 2015). Autonomic mimicry refers to any conjoined physiological patterns within the group or dyad (e.g., heart rate (Riddoch and Cross, 2012), skin conductance (Behrens et al., 2020), pupil diameter (Kret et al., 2014), or hormonal level (Liu et al., 2005)).

2. Why do we mimic: the affiliative account

Mimicry – in its numerous and different forms – has been observed among several species such as humans (Chartrand and van Baaren, 2009), great apes (Bertini et al., 2022; Fuhrmann et al., 2014; Palagi et al., 2007; van Berlo et al., 2020), Old World monkeys (Mancini et al., 2013; Scopa and Palagi, 2016; Whitehouse et al., 2016), meerkats (Palagi et al., 2019), lemurs (Valente et al., 2022), dogs (Harr et al., 2009; Palagi et al., 2015), pigs (Norscia et al., 2021), sun bears (Taylor et al., 2019), dolphins (Jaakkola et al., 2010; Reiss and McCowan, 1993), and budgies (Miller et al., 2012). The widespread phylogenetic roots of mimicry have attracted considerable interest from researchers seeking to comprehend its underlying function and adaptive significance. A classic proposal for why we mimic is that mimicry occurs in order to affiliate and bond with conspecifics, within the context of the Social Glue hypothesis (Lakin et al., 2003). Lakin et al. (2003) suggest that the function of mimicry may have evolved over time, eventually serving as a mechanism for fostering affiliation (Lakin et al., 2003). According to the Social Glue Hypothesis, initially, mimicry may have served a survival function: the behavior displayed by conspecifics conveys vital information about the environment, such as the presence of predators, prey, or dangers. The ability to imitate those behaviors, through a perception-behavior link (Box 1), was thus critical for survival, and individuals with such tendencies were favored by natural selection (Chartrand et al., 2005). Lakin et al., (2003) suggested that, in absence of threats (e.g., predators), the function of mimicry may have shifted from survival towards *social* survival, fostering social bonding and increasing affiliation. The authors have presented substantial evidence in favor of the Social Glue hypothesis, which has been further corroborated by recent research. We are aware that survival and social bonding may not be a dichotomy, as social bonding is crucial for group-living species. We also acknowledge that the empirical support for the link between mimicry and affiliation (or positive affect) is not straightforward and still the object of debate in the field. We will explore research beyond this perspective – both for human and non-human animals – in **Section 3** .

In support of the Social Glue hypothesis, previous studies have shown that being mimicked in facial expressions and mannerisms leads to more likeability of the partner and smoothness of the interaction (Chartrand and Bargh, 1999; Lakin et al., 2003), even when the mimicker is a virtual agent (Fasya et al., 2024). The automatic process of mimicry can also affect more complex cognitive processes (e.g., trust). In a negotiation task, Wessler et al. (2024) found that participants trusted the confederates significantly more when they mimicked their facial expressions, posture, gestures, and eye gaze than when they did not (Wessler et al., 2024). Beyond motor mimicry, autonomic pupil dilation mimicry has been associated with increased trustworthiness and pleasantness toward a virtual partner (Kret et al., 2015; Kret and De Dreu, 2017; Wehebrink et al., 2018a). These positive effects are more salient when mimicry is purposefully manipulated. In a dyadic study, Stel and Vonk (2010) observed that instructing one of the participants to suppress mimicry resulted in demoted smoothness and closeness of the interaction (Stel and Vonk, 2010). Similarly, covertly manipulating smile mimicry during free online interactions causally modulated the emergence of romantic attraction and influenced how participants vocally synchronized with each other (Arias-Sarah et al., 2024). While these studies showed how mimicry can enhance affiliation and trust, research has also explored the reverse relationship, showing that

Box 1
How do we mimic.

The underlying mechanism behind mimicry has traditionally been attributed to the Perception-Behavior Link: observing someone perform a behavior would trigger the mental representation of that behavior, subsequently increasing the likelihood that the observer will engage in the same behavior themselves (Chartrand and Bargh, 1999). The perceptual activity extends to behavioral representations, thereby increasing the likelihood of mimicking the observed behavior without conscious awareness. Essentially, overlapping brain areas are engaged during both the execution and observations of motor actions (Bertini et al., 2022). This notion is supported by research demonstrating the activation of mirror neurons during both action execution and observation (Fuhrmann et al., 2014). This proposal considers the brain as a stimulus-response mechanism, which may be oversimplified when applied to humans. Rather, the brain seems to operate as a generative system accumulating affective information over time via a cross-modal activation of multi-sensory representations (Wood et al., 2016). A more comprehensive explanation is provided by the Neurocognitive Model of Emotional Contagion (NMEC). In this model, an individual's emotional state resonates in non-verbal motor movements and physiological responses. Upon perceiving the target's state, the observer's neural representations are activated, potentially resulting in motor and autonomic mimicry. This process may lead to emotional contagion (Prochazkova and Kret, 2017a). It is important to note that, particularly for non-human animals, the simpler Perception-Behavior Link may still be more parsimonious in explaining mimicry. As Gruber and Grandjean (2017) discuss, it remains debated whether facial expressions and other signals in non-human animals are used for communicative purposes or are uncontrolled emotional expressive signals. The function may depend on context and the type of signal being mimicked. In non-human animals, and partially also in humans, it is challenging to prove that a mimicked expression (e.g., a play face) actually reflects the presumed emotional state or leads to emotional contagion. The degree of automaticity and emotional content in mimicry likely varies across species and contexts. These considerations highlight the complexity of understanding mimicry across the animal kingdom and the need for caution when applying human-centric models to other species.

pre-existing affiliative bonds can influence the extent of mimicry. Evidence suggests a significant ingroup advantage in facial mimicry (Likowski et al., 2012; Seibt et al., 2015). This phenomenon is characterized by individuals exhibiting stronger mimicry responses to facial expressions of ingroup members compared to those of outgroup members. Notably, this effect appears to be particularly pronounced for negative emotional expressions (Bourgeois and Hess, 2008; van der Schalk et al., 2011a). For instance, van der van der Schalk et al., 2011a observed enhanced mimicry of fear and anger expressions when displayed by ingroup members relative to outgroup members. On a similar line, previous research found that mimicry can be boosted by the attempt to affiliate (Lakin and Chartrand, 2003), the pre-existing liking (Stel et al., 2010), and the pre-existing bond (e.g., with a romantic partner, Maister and Tsakiris, 2016) towards the interaction partner.

The Social Glue hypothesis, primarily grounded in human studies, posits a link between mimicry and social affiliation. Although not exclusively, it is important to consider that the human mimicry literature predominantly focused on enacted expressions and computer tasks, which challenges their ecological validity. On the other hand, research on non-human animals typically has more ecological validity, allowing observation of behaviors in more naturalistic contexts. While the direct connection between affiliation and mimicry has been less explored in non-human animals, there is growing evidence of mimicry's positive effects in various social species other than humans. For instance, Roth et al. (2021) have proposed that coordinated behaviors, which may include various forms of mimicry, could serve as a foundation for pair bonding in diverse animal species. By reviewing findings on inter-individual coordination and pair-bond formation, maintenance, and bi-parental care across various species, the authors suggest a positive feedback loop between interpersonal coordination and pair-bond strength, where mutual displays and coordinated behaviors reinforce the bond between partners (Roth et al., 2021). Beyond pair bonding, several studies on non-human animals have observed positive consequences of mimicry. For instance, a study showed that when geladas (*Theropithecus gelada*) engaged in rapid facial mimicry of play-face – a notorious playful facial expression – the play session lasted significantly longer compared to when they did not mimic each other (Mancini et al., 2013). A similar result has been found for slender-tailed meerkats (*Suricata suricatta*) (Palagi et al., 2019), south American sea lions (*Otaria flavescens*) (Llamazares-Martín et al., 2017), and domestic dogs (*Canis lupus familiaris*) (Palagi et al., 2015), in which the mimicry of relaxed open mouth correlated with prolonged sessions of play fighting. A prevalent interpretation of these findings suggests that mimicry may function to reduce the ambiguity inherent in interactions, consequently moderating potentially aggressive escalation of play interactions (Palagi et al., 2019), especially in species that have a very competitive form of play-fighting (Llamazares-Martín et al., 2017). For Slender-tailed meerkats, relaxed open-mouth display without mimicry did not have the same effect on play duration, stressing even more the role of mimicry in boosting affiliation in social interactions (Palagi et al., 2019). The bi-directionality of the mimicry-affiliation link has been observed also in non-human animals. Previous research on domestic dogs (*Canis lupus familiaris*) showed an effect of familiarity on the mimicry of play-face and play bow, with mimicry being the highest among "friends" conspecific, followed by acquaintances and then strangers (Palagi et al., 2015). Similarly, in several species, contagious yawning seems to occur more often between siblings or socially close individuals (domestic pigs (Norscia et al., 2021); geladas (Palagi et al., 2009); bonobos (Demuru and Palagi, 2012); humans (Norscia et al., 2020)), suggesting mimicry as a potential basis for emotional contagion, but see (Massen and Gallup, 2017; Neilands et al., 2020; Valente et al., 2022). Further, some authors compared mimicry of play-face in socially tolerant Tonkean macaques (*Macaca tonkeana*) versus the relatively intolerant Japanese macaques (*Macaca fuscata*): mimicry was absent in the latter species, whereas in Tonkean macaques it was present and critical for play duration (Scopa and Palagi, 2016). Play sessions in Japanese macaques are competitive, with rather little physical contact due to the inflexible ranked social structure. Therefore, the authors attributed the lack of mimicry to the absence of an affiliation goal hindering the basis for emotional contagion to emerge (Scopa and Palagi, 2016, but see Facondini et al., 2024).

Building on the mimicry-affiliation link, Hess and Fischer (2022) introduced a fresh perspective on the function of mimicry, conceptualizing it as a social regulator. They define mimicry as the imitation of affiliative non-verbal behavior with the goal to affiliate (Hess and Fischer, 2022). Mimicry here is framed as a social act that is based on emotional appraisal – the process of evaluating the emotional significance of a situation or stimulus – and tied to an affiliative context or goal. This view suggests that mimicry occurs when an emotional expression is interpreted as a signal directed at oneself, the expresser is perceived to have affiliative intent, and the mimicker also has affiliative intent. Hess and Fischer's model assumes that mimicry is based on emotional understanding, meaning that we tend to mimic what we understand rather than merely replicate what we observe. As such, the authors narrow the landscape of mimicry only to emotional mimicry. Emotions arise from the appraisal of the events that trigger them, shaped by the expresser's drivers. Therefore, emotional expressions are intrinsically meaningful, but behaviors such as finger tapping and face touching do not carry such meaning. The social regulator theory revolves around three main assumptions: mimicry is goal-dependent, and this goal is mostly affiliative; its occurrence depends on the perception of an emotional expression as affiliative; and people mimic the meaning of an emotional expression rather than the specific muscle movements (Hess and Fischer, 2022). Studies on cross-modal mimicry corroborate the latter assumption, showing that facial mimicry may occur in response to prosody (Hawk and Fischer, 2016) and body posture (Moody et al., 2018). As evidence that mimicry depends on an affiliative goal, the authors remarked on the dependency of mimicry on liking (Salazar Kämpf et al., 2018), physical similarity (Olszanowski et al., 2022), and a cooperative goal (Seibt et al., 2015), as well as the increased mimicry occurrence for affiliative facial expressions compared to non-affiliative (Olzanowski and Topilo, 2024). Moreover, it has been shown that having the goal of inferring the emotional state of others can indeed enhance the mimicry of different facial expressions (Murata et al., 2016). In response to studies that found evidence for the mimicry of negative emotional expressions (Hühnel et al., 2014; Murata et al., 2016; van der Velde et al., 2010), Hess and Fischer have argued that the mimicry of antagonistic emotions may not mimicry at all, but rather represents an emotional reaction to the expression of the other (Hess and Fischer, 2014)

To conclude, the Social Glue hypothesis (Lakin et al., 2003) and the social regulator theory (Hess and Fischer, 2013) provide compelling frameworks to understand how mimicry is linked to affiliation, trust, and group cohesion, thereby potentially increasing individual survival and fitness. While the affiliative function of mimicry is well-supported, our perspective paper suggests that multiple ultimate causes likely coexisted and contributed to the selection of this behavior across various species. As we delve deeper into the literature in Section 3, it becomes clear that the evolutionary story of mimicry may be more nuanced than initially proposed.

3. Evidence beyond the affiliative account

The previous section summarized the main theories framing the ultimate function of mimicry – *why* we mimic – as related to affiliation. However, a closer look at the literature reveals several gaps that make the affiliative function of mimicry only partially accountable. The absence of a clear causal direction in the mimicry-affiliation link makes it challenging to determine whether affiliation is truly an ultimate cause of mimicry or a byproduct of more self-beneficial causes. Furthermore, making mimicry entirely dependent on a social goal implies that emotional expressions should always have a communicative function, which may not always be the case, even if they have communicative value (Curtis et al., 2011; Susskind et al., 2008). Emotional expressions can occur without any intent to communicate, yet they may still be mimicked. In this regard, we believe that excluding all negative, ambiguous, or neutral expressions from the mimicry landscape may limit our ability to develop a comprehensive understanding of mimicry's adaptive value. Indeed, even Hess and Fischer (2022), in proposing their social regulation model, acknowledged that numerous questions remain about the role of mimicry in negative interactions. To address these concerns, we will explore the following points: I. Mimicry is not bound to positive expressions; II. Mimicry does not invariably depend on an affiliative social goal; III. The affiliative effects of mimicry may be a secondary consequence after a more self-beneficial effect of the mimicker.

3.1. *Mimicry is not bound to positive expressions*

Hess and Fischer (2014) proposed a sharp distinction between the mimicry of affiliative emotional expressions and other non-affiliative behaviors, categorized as mere reactions (Hess and Fischer, 2014, 2022). We argue that a more fluid interpretation of mimicry might better represent the complexity of the phenomenon. Especially in the attempt to understand the ultimate causes of mimicry, it is important to include mimicry of expressions that vary in adaptive significance. These include negative expressions (Iki and Kutsukake, 2021; Murata et al., 2016; Rauchbauer et al., 2016) and context-dependent expressions, whose emotional valence can shift based on the context in which they are produced (Kret, 2015; Leone et al., 2014). In the human domain, mimicry of negative facial expressions has been observed in several studies (Hühnel et al., 2014; Murata et al., 2016; van der Schalk et al., 2011; van der Velde et al., 2010). Although acknowledging the limitations of investigating mimicry of negative expressions with EMG (van der van der Schalk et al., 2011a), it is noteworthy that mimicry of these expressions has still been observed in such well-controlled lab studies. Murata et al. (2016) found that participants mimicked different facial expressions – including anger, fear, and disgust – especially when primed with the goal of inferring the emotional state of the target (Murata et al., 2016). Mimicry of angry facial expressions has been detected in multiple studies (Hühnel et al., 2014; Kret et al., 2013; van der Schalk et al., 2011a), and it has been shown to result in less liking (van der Velde et al., 2010). Other authors investigated the effects of angry facial expressions on other forms of mimicry (Rauchbauer et al., 2016). Specifically, this study revealed that mimicry of finger movements was enhanced when participants were exposed to angry outgroup faces compared to happy outgroup faces (Rauchbauer et al., 2016), suggesting that negative emotional expressions can also influence mimicry across different modalities. Similar findings can be observed in the autonomic domain: constricted pupil size – an emotional cue that could signal fatigue, boredom, or social disinterest – has been shown to be mimicked and to decrease trust (Kret and De Dreu, 2017; Prochazkova et al., 2018a; Wehebrink et al., 2018). In the context of angry facial expressions, constricting pupil sizes foster even more pupil constriction mimicry. Opposing effects were found for happy faces and dilating pupils (Kret et al., 2015).

Finally, although limited, some studies report that attending to angry faces (Campellone & Kring, 2013) and mimicking scratching and yawning (Diana et al., 2023) correlates to lower level of trust. These effects are not consistent in the literature (Olzanowski and Topilo, 2024; Rymarczyk et al., 2016) and need further replication. We believe there are multiple explanations for this inconsistency: first, the outcomes of negative mimicry have been largely overlooked in the literature, with predominant attention given to affiliative expressions. Furthermore, unlike affiliative expressions, negative expressions likely require higher metabolic costs (Wood et al., 2016). Therefore, in non-threatening environments (e.g., computer tasks in the lab), the need for defensive responses like mimicry of negative emotional expressions may be significantly diminished. As a result, any observed mimicry in these situations might not accurately reflect the typical behavioral responses to genuine threats in naturalistic settings. In contrast, non-human animal studies provide a robust framework for exploring behaviors that are challenging to elicit in a lab setting or to observe in humans in the wild. Biological studies also reveal a broader range of mimicked behaviors, such as yawning, scratching, and anti-predator vigilance behavior, which are largely overlooked in human research. Given their phylogenetic conservation across various species (Gallup, 2022), as well as their contagiousness, these behaviors should not be disregarded as evidence for the understanding of the ultimate causes of mimicry.

Anti-predator vigilance behavior (e.g., sudden head raise, ear twitches), which has a distinct adaptive significance compared to other more popular contagious behaviors (e.g., play face), has been proven to be mimicked among individuals (Iki and Kutsukake, 2021; McDougall and Ruckstuhl, 2018; Pays et al., 2007). While engaging in vigilance behavior, individuals observe the surroundings to gather information on potential threats posed by predators or other conspecific (Favreau et al., 2010). In addition, they also keep a close eye on their social environment and monitor the interactions - both affiliative and agonistic - of group members (Schino and Scerbo, 2020). Therefore, mimicking vigilant behaviors is an adaptive technique to monitor and avoid threats, as it allows individuals to rapidly share information about the immediate environment. Being vigilant simultaneously can directly increase an individual's benefit as it allows it to escape from predators faster. Just as other contagious behaviors, vigilance contagion has been shown to be affected by social biases. For instance, a study on Japanese macaques showed that vigilance was contagious to lower-ranked compared to high-ranked individuals, and also more contagious to mothers when expressed by their offspring (Iki & Kutsukake, 2021). To further prove that this behavior is actually contagious, and not a mere synchronized reaction to an external stimulus, a study on bighorn sheep (*Ovis canadensis*) showed that routine vigilance and contagious vigilance are qualitatively different, with the latter being characterized by quicker head raise, longer gazes and more likelihood of stop chewing (McDougall and Ruckstuhl, 2018).

Unlike vigilance behavior, whose adaptive significance in predator avoidance is well-established, the evolutionary advantages of contagious yawning and scratching remain debated (Gallup, 2022; Sanders et al., 2019). The emotional valence of yawning and scratching likely varies depending on the context in which they occur and are mimicked. This contextual flexibility makes these behaviors particularly valuable for studying mimicry in social settings. Several studies found the mimicry of scratching to increase in potentially alarming situations, such as the presence of an unfamiliar conspecific, especially in more despotic species (rhesus macaques (Feneran et al., 2013); Japanese macaques (Nakayama, 2004)) or between weakly bonded group mates (Bornean orangutans - Laméris et al., 2020)). In humans, contagious scratching increases for people who are more prone to experience negative emotions (Schut et al., 2015). Although most of the research on contagious scratching focuses on negative context, scratching behavior can increase also in positive valence situations like play (Neal and Caine, 2016), suggesting that its valence may be context-dependent. Similarly, also contagious yawning exhibits a complex relationship with social and emotional contexts. While some studies have observed contagious yawning to occur more frequently with strong social bonds (humans - Norscia and Palagi, 2011), or with familiar individuals (bonobos - Demuru and Palagi, 2012) other studies fail to find this relationship (bonobos - Norscia et al., 2022; spider monkeys -Valdivieso-Cortadella et al., 2023). Some authors even found contagious yawning accompanied by self-directed stress behaviors (Paukner and Anderson, 2006), suggesting that mimicking yawns can also be associated with negative situations. Further strengthening the context-dependency of yawning, mimicking different yawning displays can be associated with both affiliative and agonistic intent, suggesting that different configurations (or intensities) of the same behavior may have multiple effects (Leone et al., 2014). Contagious yawning and scratching share important similarities with other forms of mimicry, such as its involuntary nature and social modulation: they can both be considered forms of motor resonance that involve automatic, unconscious imitation of observed actions from the face, and they are both observed across various mammalian specie. In light of these parallels and the rich body of research on contagious yawning's social and emotional correlates (more research is needed on scratching), we believe they are overlooked expressions in psychology when investigating the broader adaptive functions of mimicry.

Due to their usefulness and adaptive function, negative or contextual-dependent emotional expressions should not be excluded from the mimicry landscape solely because they do not carry an affiliative meaning. Given the evidence for mimicry of emotional expressions that goes beyond positive valenced in humans and non-human animals, we believe that redefining the concept of mimicry according to its presumed evolutionary outcomes (e.g., true mimicry occurs when we mirror positive emotional expressions; otherwise, it is simply a reaction, Hess and Fischer, 2022) may erroneously oversimplify the phenomenon. We ascribe mimicry as a broader mechanism indicative of a shared mental state between two or more individuals. Consequently, we suggest that the occurrence of mimicry is less contingent on the emotional valence of the expression, and more on whether the observer is sufficiently triggered to mirror the shared emotion (Prochazkova and Kret, 2017a).

3.2. *Mimicry does not invariantly depend on an affiliative social goal*

The social regulation theory argues that mimicry is a social act, depending on the presence of affiliative social goals of both the mimicker and the mimickee (Hess and Fischer, 2022). The presence of mimicry in response to negative emotions presented in the previous section indicates that factors beyond affiliative goals are at play. Moreover, while mimicry can foster affiliation and social cohesions, even expressions typically associated with affiliation do not invariably result in positive social outcomes. In the abundance of studies focusing on the mimicry of smiles, it seems like only 50 % found a strong mimicry-liking link (Hale and Hamilton, 2016b). Smiles are not always of affiliative nature and can have several meanings (e.g. polite, contemptuous, nervous, apologizing), more or less ambiguous depending on the social context (Niewiadomski et al., 2010). Interestingly, mimicking different types of smiles has been shown to help reduce bias that might otherwise arise from relying solely on contextual cues (Korb et al., 2014; Ludwig et al., 2013). For instance, when individuals are prevented from mimicking observed smiles, their ability to differentiate between true and fake smiles is compromised (Korb et al., 2014). Similarly, when mimicry was restricted, individuals tended to perceive a neutral smile differently depending on the context (Orlowska et al., 2023), hinting towards the possibility that mimicry may have a more complex function beyond affiliation, even when focusing solely on affiliative non-verbal behaviors. Some authors suggested that mimicry may serve more self-interested or manipulative ends: for instance, waitresses who verbally mimicked (repeated) their customers' orders received significantly higher tips compared to those who did not mimic (van Baaren et al., 2003). Similarly, strategic behavioral mimicry of facial expressions and mannerisms can directly benefit individual gains in a negotiation task, without harming the counterpart (Maddux et al., 2008). This partially aligns with the Social Top-down Response Modulation (STORM) model (Wang and Hamilton, 2012), which suggests that mimicry is a flexible social behavior controlled by sophisticated top-down processes. Although the STORM model sees mimicry as driven by affiliation and positive social consequences, it still implies that individuals may, strategically or not, use mimicry to achieve personal goals – perhaps at the cost of others – rather than solely to foster social cohesion.

Findings that challenge affiliation as a unique motive for mimicry to occur can also be found in the non-human domain. Facondini et al. (2024) demonstrated the presence of mimicry of play face in despotic-intolerant rhesus macaques. The research revealed that mimicry extended the duration of play sessions, but interestingly, it was not affected by the strength of the 'play bond' between individuals. Instead, hierarchical position turned out to be the key factor influencing mimicry patterns, with subordinate individuals being more likely to mimic dominant subjects. The authors propose an intriguing explanation for these results, suggesting that mimicry may serve as a mechanism to reduce uncertainty arising from incongruent or absent responses during interactions, potentially minimizing misunderstandings and preventing conflict escalation (Facondini et al., 2024). Correspondingly, another study found that play-face mimicry was preceded and followed by more offensive playful patterns, yet it still prolonged play sessions (Spyder Monkeys - Cordoni et al., 2024). These findings are critical for two reasons. First, they prompt us to rethink the nature of play interactions. Most of the literature on mimicry in non-human animals comes from the sphere of playfighting, which has traditionally been considered a "positive" interaction. However, this may not necessarily be the case. Play oscillates between competition and cooperation, encompassing a spectrum of behaviors in between (Cordoni and Norscia, 2024). Consequently, when investigating the potential social outcomes of mimicry in behavioral spheres like playfights, the mixed valence of these social contexts must be taken into account. Second, these results demonstrate that even typically affiliative expressions such as a smile or play face are not invariably mimicked to affiliate. Instead, mimicry may foster more competitive interactions by increasing the predictability of other individuals while reducing behavior misinterpretation.

Collectively, this evidence in human and non-human animals shows that an affiliative social goal may not be necessarily a pre-requisite for mimicry to occur. Instead, mimicry seems to ease the prediction of the environment, including the social environment. Because we like our world to be predictable, this oftentimes yields positive social outcomes. But not always.

3.3. *Benefits of mimicry for the mimicker*

We argue that for mimicry to be evolutionarily adaptive, it should not be unequivocally bound to an affiliative social goal. It is possible to see prosocial consequences of mimicry, without that being the core function. Thus, while we recognize and acknowledge that increasing affiliation could itself be an advantage for the mimicker, we believe that mimicry may entail other advantages that go beyond affiliation. Many expressions are functional to the circumstances in which they are performed. We acknowledge that increasing affiliation could itself represent an advantage for the mimicker and the overall group. Positive expressions (e.g., smile, play face, dilated pupils) may have direct benefits related to affiliation, and it is logical that the mimicry of such expressions increases social bonding. However, negative emotional expressions also have benefits for the individual as they may have a protective function. For instance, widening the eyes during a fearful expression enhances the perception of the visual field (Susskind et al., 2008). Disgust has a direct benefit for survival by eliciting eyes and nose closure, and tongue protrusion to let out toxic material (Curtis et al., 2011). An angry facial expressions may be beneficial to potentially deterring threats or asserting dominance in social interactions (Tay, 2015). Mimicking those expressions can be evolutionarily advantageous for the survival of the individual. Imagine a scenario where an individual mimics the fearful expression of a peer in a group setting. While mimicking the widened eyes of their peers, individuals can better perceive potential threats and respond appropriately, either by offering support or by avoiding potential danger. Vigilance serves again as a good example. By mimicking conspecific exhibiting signs of heightened vigilance (e.g., sudden head raise, ear twitches), even individuals who have not directly perceived a threat can benefit from the heightened state of alertness. Similarly, in the context of non-human animals, mimicking scratching may signal an increase in the overall stress of the group and facilitate the detection of the stressor (e.g., an unfamiliar conspecific) (Laméris et al., 2020). Further supporting this notion, a recent study by Gallup and Wozny (2024) demonstrated that exposure to yawning faces enhanced the detection of potential threats in the environment. Specifically, participants who viewed videos of people yawning were quicker to identify images of spiders and cockroaches in a visual search task compared to those who viewed neutral faces (Gallup and Wozny, 2024). This finding suggests that contagious yawning may serve an adaptive function by increasing vigilance and improving the detection of potential threats.

It is worth considering that positive and negative mimicry share substantial neural correlates, even though research has primarily focused on facial expressions (Likowski et al., 2012; Rymarczyk et al., 2018). Studies combining mimicry with neuroimaging techniques have consistently found that mimicry of diverse emotions, including happiness, anger, and sadness, but also pupil mimicry, activate core regions of the mirror neuron system (MNS), particularly the inferior frontal gyrus (IFG) (Likowski et al., 2012; Prochazkova et al., 2018b; Rymarczyk et al., 2018). While some emotion-specific variations in activation patterns exist, the fundamental neural processes underlying mimicry appear to be consistent across different emotional valences. This suggests that at least several forms of mimicry, regardless of the specific emotion being expressed, rely on a common neural framework involving both motor simulation and emotional processing areas. Recent research provided compelling evidence for the involvement of mirror neurons in negative social behaviors. Yang et al. (2023) showed that neurons in the ventromedial hypothalamus (VMH) of mice exhibit some mirroring properties for the aggression performed by self and others (Yang et al., 2023). These neurons were active both when mice engaged in fighting and when they observed aggressive interactions between others. This finding challenges the traditional view of mirror neurons as primarily supporting empathy. Ferrari et al. (2024) expanded on these implications, suggesting a need to rethink the unidirectional link between mirror neurons and empathy. This “dark side” of mirror neurons points to their role in a wider spectrum of social interactions, including competitive and potentially threatening ones (Ferrari et al., 2024). The traditional focus on mirror neurons as mechanisms of empathy may have inadvertently created a bias towards affiliative expressions and social contexts, leading to the investigation of positive mimicry while overlooking the potential role of negative emotional mimicry. In summary, the evidence for individual benefits derived from some expressions, combined with the involvement of mirror-like mechanisms and overlapping networks in both positive and negative social behaviors further supports the notion that mimicry serves a more complex purpose than mere affiliation.

Existing theories provide valuable insights into the ultimate cause of mimicry, but they do not fully capture its complexity. We aim to introduce a more nuanced, fundamental role for mimicry. During social interactions, individuals exchange a variety of multimodal emotional signals and cues: regardless of whether they are consciously expressed, others often mimic them. While mimicry is frequently associated with social bonding, limiting its function to affiliation fails to fully account for a significant portion of the literature across human and non-human domains. We suggest that mimicry – both in the present and throughout its evolutionary trajectory – functions to facilitate the prediction of the environment including conspecifics’ behavior, yielding immediate advantages for the individual. This alternative perspective recognizes mimicry as a broader mechanism indicative of shared mental states. This approach acknowledges the multifaceted nature of mimicry and its potential direct benefits for the mimicker, benefits that can then also be advantageous to the group as a whole.

4. The predictive social brain and mimicry

In dynamic environments characterized by frequent changes, preparedness constitutes a great evolutionary advantage. To ensure energy efficiency and enhance our adaptive responses, the brain utilizes past experiences to generate predictions, thereby reducing the impact of unexpected outcomes (Nave et al., 2020). This idea is generally referred to as Predictive Processing (PP) or the Bayesian brain. In the PP framework, the brain operates as a probabilistic machine continuously constructing models of the world to anticipate and interpret incoming sensory information. To optimize behavior and learn from mistakes, the brain constantly updates these models to minimize the discrepancy between expectations and experience – the *prediction error* (Friston, 2012). Through the limbic cortices, predictions about sensory events are issued across various sensory modalities (Chanes and Barrett, 2017). These predictions activate neuronal discharge in regions primed for emotional responses while concurrently processing real-time sensory inputs. Predictions act as hypotheses regarding the environment, tested against incoming sensory data (Kilner et al., 2007). Any deviations between prediction and sensory input are flagged as prediction errors, prompting corrective actions by the brain. While the critical role of predictive mechanisms in motor control, perception, and learning is extensively documented, an expanding body of research has already begun to demonstrate that the brain may use PP in the social and affective domains (Brown and Brüne, 2012; Thornton et al., 2019). A pivotal model on the human mirror neuron network proposes that predictive coding of others' actions may contribute to inferring their intentions (Kilner et al., 2007). Within this framework, the brain uses probabilistic associations between traits, mental states, and actions to generate predictions about others' future behavior (Tamir and Thornton, 2018). This predictive process involves both bottom-up sensory input and top-down expectations. The top-down expectations refer to the predictions and prior beliefs about the behavior that the brain generates in higher-level cortical areas and then projects down to lower-level sensory areas. These top-down predictions are based on previous interactions, statistical regularities, and contextual information (Brown and Brüne, 2012). The bottom-up sensory input includes the visual, auditory, and other perceptual cues you pick up on when observing another person's facial expressions, body language, tone of voice, and behaviors *in the moment*. This raw sensory data is processed in a feedforward manner from lower-level sensory cortices up through higher-level association areas (Chanes and Barrett, 2017). The brain then compares this bottom-up sensory information to the top-down social predictions. Any mismatch or "prediction error" between what you expected and what you observed generates an error signal that can be used to update your internal models of the other person's mental state and surrounding environment. We believe mimicry – via somatosensory simulation – may contribute to minimizing these prediction errors (Fig. 1). Within this framework, perception and action are interconnected (Hutchinson and Barrett, 2019): via sensorimotor simulation, an organism gets vital information from the environment to act adaptively, also in the absence of prior information.

Imagine meeting your coworker Alex at a party. Based on your past interactions, you have top-down expectations about their typical non-verbal behavior, like an open posture, eye contact, and a friendly expression when greeting people at social events. As Alex approaches, your brain starts processing the bottom-up sensory input – the actual non-verbal behaviors you observe, such as their body language and facial expression. You may unconsciously mimic some of Alex's visible emotional signals – facial expressions, body postures, tone of voice – and other physiological parameters, such as heart rate, blushing, or pupil size. If Alex's actual behavior matches your expectations, your brain perceives this as a confirmation of your predictions. However, if their behavior does not align with your predictions – for example, they avoid eye contact and are frowning – your brain generates a prediction error. This mismatch prompts your brain to update its understanding of Alex's current mental state and adjust its predictions. By unconsciously mimicking Alex's behavior – both on a behavioral and autonomic level – the proprioceptive feedback from your own body provides additional bottom-up information. This mimicry helps you quickly recalibrate your internal model, reducing the prediction error between your expectation of positive interaction and the actual tense atmosphere. This continuous feedback loop reduces the mismatch between sensory input and prediction. One literally becomes more similar to the other, making them, and consequently the surrounding environment, easier to predict (Kret and Akyüz, 2022). Therefore, mimicry may play the role of a corrective mechanism to mitigate prediction errors, as it generates responses that mimic observed sensory inputs, aiding cortical networks in updating their predictions. It is crucial to note that mimicry's role in predictive processing extends beyond inferring others' internal states. It may also aid in predicting and responding to environmental cues. In the case of Alex, while your initial focus was on predicting their internal state, mimicking their expressions of concern could also heighten more quickly your awareness of potential stressors or threats in the shared environment. This dual function of mimicry - informing us about both the individual and the environment - underscores its efficiency as a predictive mechanism in social interactions and beyond.

A recent review by Waller et al. (2017) suggests that a similar predictive framework may also apply to primate facial expressions (Waller et al., 2017). They conclude that, while attending and reacting to others'

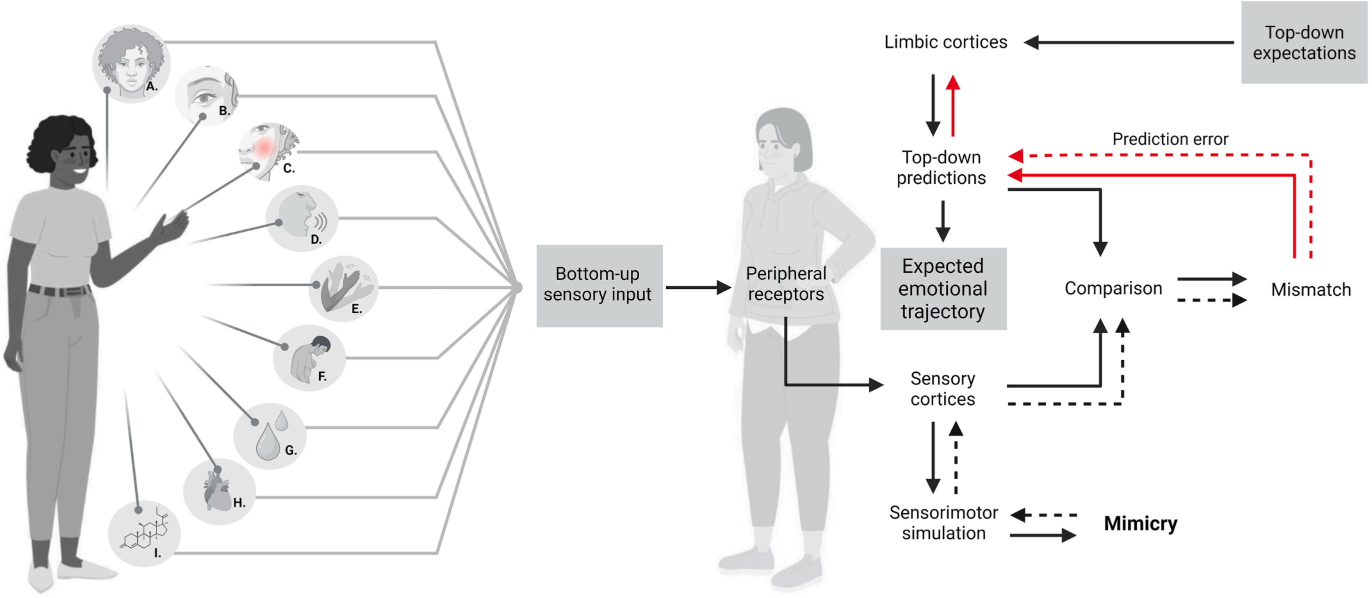

Fig. 1. Schematic representation of the predictive account of mimicry. The target is sending a variety of non-verbal signals and cues such as: A. facial expressions; B. changes in pupil size and eye-gaze; C. blushing; D. vocal signals; E. gestures; F. posture; G. changes in electrodermal activity; H. changes in cardiovascular activity; I. changes in hormonal levels. These bottom-up sensory inputs are received by the peripheral receptors of the receiver. While the signal is sent to the sensory cortices (solid black lines), the limbic cortices issue top-down predictions based on previous interaction with the target, statistical regularities, and social context. These top-down predictions are compared with the bottom-up sensory inputs and, if there is a mismatch, a prediction error is issued (solid red line) through the limbic cortices that update the predictions in a feedback-loop manner. If the receiver mimics those emotional expressions (dotted black line), it will add more information to the bottom-up predictions via sensorimotor simulation (dotted black lines), resulting in a lower mismatch and reduced prediction error (dotted red line).

emotions may not be the most parsimonious explanation for the evolution of facial expressions, anticipating and preventing harm by predicting others' behavior might have had extensive selective pressure on the emergence of facial expressions. The authors challenge the fundamental assumption that facial expressions may correspond to an affective state, suggesting that the differential neural responses observed for various emotional expressions may be attributed to the valence of the emotional expressions instead of salience (e.g., it is more adaptive to quickly respond to fear than to happiness) (Waller et al., 2017). Consequently, they critique the concept of emotional contagion and mimicry, asserting that, from a functional standpoint, it seems improbable that the default response to another's facial expression should *consistently* mirror the sender's. Their argument primarily lies in the fact that, in many species, facial threats often elicit formal signals of subordination and/or avoidance rather than reciprocal threats (Waller and Micheletta, 2013). We acknowledge the debate surrounding the relationship between emotional expressions and internal emotional states (Crivelli and Fridlund, 2019; Gruber and Grandjean, 2017). As Gruber and Grandjean (2017) highlighted, while there are similarities in emotional expression across primates, including humans, there are also important differences in the underlying neural mechanisms and the degree to which expressions reflect internal emotional states. However, although Waller et al. (2017) raise important points about the functional aspects of facial expressions, we believe that completely disentangling facial expressions from the affective framework may be inaccurate. In fact, several studies support the connection between facial expressions and emotional states, at least in humans. Facial expression perception is related to specific neural activity responsible for the detection of emotional change that differs from general "visual" processing (Kovarski et al., 2017) or from processing neutral faces (Adolphs et al., 1994). Tamietto et al. (2009) further demonstrate that emotional contagion can occur even without conscious awareness of facial expressions. They found that passive exposure to unseen expressions still triggers fast, affective reactions, suggesting that emotional responses to expressions may be mediated by evolutionary pathways that bypass conscious processing (Tamietto et al., 2009). Additionally, the direct neuromuscular stimulation of facial muscles can influence emotional experience: by activating specific muscles associated with smiling or frowning, authors observed corresponding shifts in felt emotion and physiological responses (Efthimiou et al., 2024). Furthermore, the argument that Waller et al. (2017) posit about mimicry is applicable only when facial expressions are taken in isolation from the context and from other non-verbal cues: facial responses, as well as mimicry, can be modulated by social context (Seibt et al., 2015), consciously or unconsciously regulated based on social norms, personal beliefs, or situational demands (Duffy and Chartrand, 2015). Besides, other non-verbal signals and cues play pivotal roles in interpersonal communication: they can complement or contradict facial expressions, providing additional layers of meaning and context to social interactions. While individuals may not mimic certain aspects of another person's behavior, such as facial expressions, they may also engage in other types of mimicry that better align with the situational demands or their own emotional states. This adaptive flexibility in mimicry facilitates effective communication and social cohesion across diverse settings. Although Waller et al. theoretical assumptions may diverge from ours, we believe our position about mimicry complements nicely with predictive accounts for the facial expressions they proposed: if emotional expressions evolved to increase the predictability of individuals (Kret et al., 2020; Waller et al., 2017), therefore increasing survival chances, mimicking such expressions – and the corresponding multi-modal or autonomic visceral inputs (Prochazkova and Kret, 2017) – may catalyze these predictions. Differently from the definition of mimicry that is embraced by Waller et al. (2017), our predictive processing perspective sees mimicry not as an automatic reflexive process that occurs regardless of the context, but rather as a more nuanced unconscious mechanism favoring internal alignment among individuals (Palagi and Scopa, 2017; Prochazkova and Kret, 2017b). Crucially, we are not suggesting that mimicry *alone* predicts others' behavior but that mimicry – by helping mitigate the prediction error – enhances inter-individual emotional bridges (Palagi and Scopa, 2017) allowing us to make more efficient predictions about them. In line with this, several studies have shown that mimicry, by giving access to multi-dimensional proprioceptive cues, accelerates emotion recognition (in women - Stel and Vonk, 2010), especially in the case of ambiguous (Halberstadt et al., 2009) or fake (Korb et al., 2014) facial expressions, but see (Folz et al., 2023). Particularly facial mimicry has been shown to speed up the recognition of emotions in others by engaging the embodied simulation processes involved in understanding those emotional expressions (Wood et al., 2016). Moreover, this proposal aligns with a recent review suggesting that predictive coding mechanisms within the parieto-insular network facilitate shared representations of others' actions and emotions (Ishida et al., 2015). Although Ishida et al. (2015) focus on self-other body representation, their model provides a neurobiological explanation of how predictive coding can facilitate shared embodied states between individuals. This network, which integrates sensory and affective information, supports our hypothesis that mimicry, by reducing prediction error, may strengthen these shared representations enhancing our ability to anticipate others' behavior, particularly in ambiguous contexts.

4.1. Mechanism of the predictive account of mimicry

The idea that mimicry may reduce prediction error is not new. In their review of the mechanism of mimicry, Hale and Hamilton (2016a) outlined a model – the Similarity model – that associates mimicry to the predictive brain, although still within the affiliative framework and in the context of *being mimicked* rather than mimicking (Hale and Hamilton, 2016a). The Similarity model assumes that a mimicked action is more rewarding than a non-mimicked one because the kinematic overlap of mimicry eases the prediction of action patterns, resulting in a low prediction error (Hale and Hamilton, 2016a). Consistent with our predictive account of mimicry, the Similarity model postulates the brain as a predictive machine anticipating forthcoming sensory inputs (Friston, 2012; Kilner et al., 2007) and finds predictable inputs rewarding. The mechanism of the Similarity model is explained by referring to Kilner et al. (2007) Bayesian perspective of the Mirror Neurons System (MNS): using the experience of their own behavior and the social context, the MNS operates as a generative model to predict the behavior of the other person and compare it to the actual behaviors (Kilner et al., 2007). In other words, the same model used to predict the somatosensory activation of each own behavior can also be used to decode the behaviors of others. Despite its focus on being mimicked and its focus on affiliation, we see some overlap between the mechanism postulated for the Similarity model and our predictive framework of mimicry. In fact, the predictive model of the MNS offers a compelling explanation for the mechanism underlying how mimicking can reduce prediction error (Kilner et al., 2007; Prochazkova and Kret, 2017). The motor signals and autonomic cues emitted by an expresser (e.g., changes in pupil size and facial expressions, cardiovascular responses, blushing) are implicitly detected by the receiver. When the sensory information arrives at the body's receptors, the brain issues multisensory predictions through the cortex. The limbic cortices (e.g., anterior cingulate cortex, ventral anterior insula, parahippocampal gyrus), with their relatively undifferentiated laminar structure, send predictions to the more highly laminated sensory cortices (for a detailed explanation, see (Hutchinson and Barrett, 2019)). These predictions trigger the relevant neural networks to prepare for the expected emotional trajectory while processing the incoming sensory input (Hutchinson and Barrett, 2019). Therefore, the predictions act as hypotheses about the environment, which are compared against the actual sensory input. Any discrepancy in this test is flagged as a prediction error. By producing a response that mimics the observed sensory input, the prediction is sent back along the cortical connections enabling the brain to update the predictions through an iterative feedback loop.

This framework allows organisms higher flexibility (Kilner et al., 2007), which is evolutionarily desirable in complex environments: by combining different autonomic inputs with emotional expressions, the brain operates as a generative system that estimates others' emotions based on emotional information gathered from *past* experiences – or prior information about the interaction partner (Halberstadt et al., 2009) – and uses them to guide our actions and representations in the *present* context. Such a paradigm partially resonates with the sensorimotor account for mimicry, which argues that mimicking an emotional expression activates a multi-modal sensorimotor simulation of that emotion (Wood et al., 2016). The activation of one element of an emotional state, such as a facial expression, can then trigger a cross-channel simulation of other emotional modalities. Given the often partial nature of input from one modality, the brain integrates information from other sensory modalities to generate predictions to round off the initial input (Driver and Noesselt, 2008). For instance, facial redness and sweating are not exclusively positive or negative (although they can be), but their valence is attributed based on additional visual input (e.g., facial expression) (Kret, 2015). Therefore, neural predictions work as a dynamically changing filter, shaping how sensory inputs are processed, and flexibly influencing the significance and further analysis of those inputs (Hutchinson and Barrett, 2019). By means of motor and autonomic mimicry, together with top-down influences and prior or contextual information, emotional meaning can be transferred from one individual to another, allowing the brain to generate faster and more accurate predictions about the environment and other individuals. This mechanism is consistent with the idea that action and mental events in the brain are constructed by giving significant weight to metabolism and energetics, with the aim of minimizing free energy in the brain and increasing efficiency (Friston et al., 2017). By rapidly adopting the internal states of others through mimicry and top-down influences, the brain can update its internal model to better match sensory input, reducing uncertainty and surprise, which are key components of free energy.

4.2. Selective pressure for mimicry as a catalyzer of predictions

Mimicry possibly evolved as a tool to ease predictions under several selective pressures. In a complex social landscape where uncertainty can be costly, mimicking others may act as a tool to reduce this uncertainty by enhancing a shared alignment between individuals. This shared representation enables more accurate predictions of the environment. Mimicking conspecific scratching or fearful expressions may enhance our vigilance (McDougall and Ruckstuhl, 2018; van Berlo et al., 2020), allowing us to detect and escape threats more effectively. Consequently, the need for enhanced threat detection and efficient information transfer within social groups likely exerted significant selective pressure on the evolution of mimicry. Aside from external threats, mimicry allows us to make predictions about our social environment (Wood et al., 2016), making individuals more desirable as social partners. When one mimics others, they not only become more predictable themselves (Hale and Hamilton, 2016a) but also gain insight into the behaviors and intentions of those they mimic. The selective pressure for good social partners drives the selection for mimicry because it reduces the costs of interacting with others and enhances understanding within social groups. Additionally, by refining predictions, mimicry streamlines social interactions, making the environment easier to navigate. Enhanced comprehension of others through mimicry leads to smoother navigation within social contexts, confirmed by research showing that mimicry enhances the perceived smoothness of the interaction (Chartrand and Bargh, 1999). Consequently, individuals are inclined to mimic others more frequently, reinforcing this behavior through positive feedback in the immediate context. For instance, yawn contagion of group conspecifics can help cool down the brain, increase overall vigilance, and prepare for future actions (Gallup and Gallup, 2007). Ontogenetically, by gaining insight into the behaviors and intentions of those they mimic, individuals leverage opportunities for social learning and improve their ability to navigate complex social landscapes. Within this framework, mimicry represents an advantage for those who are mimicked but also a benefit for the mimicker.

The predictive account of mimicry offers a comprehensive framework explaining the mimicry of positive, negative, and contextual-valenced expressions. For example, consider the effect of rapid facial mimicry of play face on prolonged play sessions studied in nonhuman primates (Llamazares-Martín et al., 2017; Mancini et al., 2013; Palagi et al., 2015, 2019). This effect can be understood through the lens of reducing ambiguity in social interactions. By mimicking their interaction partner, individuals not only make themselves more predictable, they also ease the predictions of their partner's emotional states. This reduces uncertainty and minimizes the likelihood of escalation into overly aggressive play fighting. The predictive framework underscores mimicry's role in making social partners more predictable, thereby fostering smoother and more efficient interactions and helping to avoid potential conflict escalation. Recent research by Facondini et al. (2024) provides support for this framework. They found that subordinate individuals were more likely to mimic dominant subjects, suggesting that mimicry may serve as a mechanism to reduce uncertainty arising from incongruent or absent responses during interactions (Facondini et al., 2024). Within this framework, affiliation can emerge as a secondary effect of mimicry: a predictable partner becomes a partner with whom individuals may feel more inclined to affiliate, as predictability fosters a sense of safety and trust. Moreover, viewing mimicry through a predictive lens may explain the bidirectional relationship between mimicry and affiliation observed in previous studies. When mimicry increases affiliation, it highlights a potential adaptive function of mimicry in social bonding, which can be seen as a secondary benefit of the predictive processes we propose. Conversely, the observation that mimicry can be higher between affiliated individuals suggests that we may engage in more mimicry with close individuals in an attempt to predict their behavior and emotional states more accurately. Differently from previous theories, the predictive account extends to the mimicry of negative emotional expressions (Kret and Akyüz, 2022). Mimicking negative expressions can confer evolutionary advantages. For instance, mirroring expressions of fear and disgust may help respectively enhance and dump sensory acquisition (Susskind et al., 2008), increasing chances of survival in the here and now. In addition, it offers valuable insights into the intentions and motivations of others. By accurately predicting and responding to negative emotions, individuals can navigate potential conflicts, assess threats, and understand more effectively when it is appropriate to end an interaction. Additionally, framing mimicry in a predictive perspective serves as a good explanation also for unconventional forms of mimicry, such as interspecies mimicry (Maglieri et al., 2020; Pedruzzi et al., 2022). For instance, humans mimicking and synchronizing with dogs (Buttner et al., 2015) may have increased accuracy in predicting the presence of predators or other dangers, so that individuals can take proactive measures to avoid harm and increase their chances of survival. Of course, the level of similarity that is reached depends also on the similarity and morphological overlap of the bodies (it is pretty tough to mimic the expressions of birds).

In summary, the predictive account of mimicry underscores its multifaceted intra and interspecific nature, encompassing both positive and negative expressions. By elucidating the adaptive functions of mimicry across various social contexts, this framework enhances our understanding of how mimicry contributes to predicting the environment around us and to successful social interactions in human and nonhuman communities alike.

5. Future perspective and considerations

An intriguing question arises: How might we rigorously examine whether mimicry contributes to the prediction of others' behavior?

Drawing inspiration from comparative studies and predictive brain methodologies, we suggest integrating mimicry assessment into established experimental designs. For instance, Morimoto and Fujita (2012) tested whether capuchin monkeys (*Cebus apella*) can use conspecifics' facial expressions to predict the emotional valence of an object. One monkey, the demonstrator, was expressing emotional reactions towards an object in a certain container. The other monkey, the observer, could not see the object in the container but could see the reaction of the demonstrator. After the container was closed, the monkey could choose which container to approach (Morimoto and Fujita, 2012). By assessing rapid facial mimicry on the observer and measuring the time used to approach the container, it could possible to investigate whether mimicry increases the speed of approach behavior towards the relevant container. Similarly, this design could be adapted to humans to examine whether mimicking another's emotional reaction increases predictive accuracy in selecting emotionally relevant options. In a computer task, Waller et al. (2016) showed crested macaques (*Macaca nigra*) videos of one individual approaching another. They manipulated the final frame to either keep it neutral, or superimpose a facial expression onto the macaque being approached (bared-teeth, open-mouth threat, or scream). The animal was then required to select one of two options: conflict-related injury or grooming (Waller et al., 2016). They showed that macaques used the facial display of conspecifics to predict the progression of the interaction (e.g., they chose a more peaceful outcome when the stimulus displayed a bare-teeth expression). As such, the authors framed facial expressions as cues to predict actions of others and to reduce uncertainty of the receiver (Waller et al., 2016). We believe that assessing facial mimicry in an experimental design such as the one formulated by Waller et al. (2016) represents an intriguing opportunity to investigate the potential impact of mimicry on the swiftness and accuracy of social prediction. Undoubtedly, implementing such a design would be more straightforward within the realm of human interactions, where mimicry could be effectively assessed through electromyography (EMG) whilst presenting naturalistic emotional expressions. Such a methodology would seamlessly align with the established paradigms of action prediction studies, renowned for investigating the mechanisms of the predictive brain. This approach could be complemented by employing Event-Related Potentials (ERPs), to meticulously track the temporal dynamics of neural activity during action prediction. Additionally, employing functional magnetic resonance imaging (fMRI) could point at brain regions exhibiting a preferential response to motion and change, thereby implicating their involvement in predictive processes (Brown and Brüne, 2012). Incorporating similar techniques into studies on mimicry could offer valuable insights into how mimicry interacts with predictive processing during social interactions. For example, we could investigate how mimicry either facilitates or disrupts the brain's ability to predict others' behaviors, thereby enhancing our understanding of the neural mechanisms underlying social prediction and the role of mimicry in refining these predictive models.

Stepping directly into the predictive *social* brain, Thornton et al. (2019) tested hypotheses derived from theoretical models of the predictive social mind by examining how people make predictions based on psychological dimensions such as rationality, social impact, and valence (Thornton et al., 2019). Mimicry could be added to this model by investigating how these dimensions scaffold social predictions and correlate with neural pattern similarity between mental states. One more point to be taken into account is the type of design generally used in mimicry research. In the predictive processing view, perception is hypothesis-driven. This means that any assumption about the external world (e.g., my friend is happy) instantaneously generates specific predictions regarding the corresponding perceptual input (Kilner et al., 2007). If there is a decent match, one's prior hypotheses are confirmed, laying the groundwork for subsequent cognitive processes. Conversely, bottom-up signals communicate prediction errors, prompting the revision of prior hypotheses until they more accurately account for the observed sensory information. Testing mimicry acts as a bottom-up signal minimizing prediction error implies that prediction error *must be* there. Although mimicry is mostly unconscious, current experimental designs – including some of our own (Behrens et al., 2020; Diana et al., 2023; Prochazkova et al., 2018) – do not take into account the power of the predictive brain in generating expectations: a large number of trials, together with equally long stimuli or inter-trial intervals, may contribute to an overall increased predictability of the experimental course. As also suggested by Hale and Hamilton (2016a), it is of pivotal importance to implement studies where contingency and predictability are meticulously controlled. By enhancing the unpredictability of our designs (e.g., by using Adaptive Design Optimization (Cavagnaro et al., 2009), and cross-modal correlations (Wood et al., 2016)), we could create experiments maximally informative and more closely resembling real-life interactions. Conversely, we could create experimental designs aiming at *exaggerating* the prediction error, for instance by delaying mimicry of different time windows or, in a similar fashion to the emotion recognition studies (Stel and Vonk, 2010; Wood et al., 2016), impairing mimicry but investigating how this is impacting the predictive processes instead. Recent work by Fasya et al. (2024) shows the potential of virtual reality (VR) in disentangling these processes by creating controlled yet immersive environments. VR offers an exceptional opportunity to test our predictive account by manipulating sensory and social cues in ways that are challenging in real-life settings, allowing precise assessment of mimicry under varied, unpredictable scenarios.

There are a few considerations to be highlighted regarding the predictive framework of mimicry. Hess and Fischer's work focuses on the distinction between emotional mimicry and behavioral mimicry based on whether the mimicked actions convey an affective meaning or not (Hess and Fischer, 2013). This distinction becomes relevant when considering how mimicry might contribute to eliciting visceral responses and reducing prediction errors. With such a sharp line between emotional versus neutral expressions, our predictive model of the function of mimicry might fail to account for mimicked behaviors that are *considered* free from affective meaning (e.g., foot tapping, finger tapping, face touching). However, we argue that such a clear dichotomy may not necessarily exist. For instance, foot tapping might be perceived as a sign of nervousness. In a situation where individuals are required to suppress their nerves (e.g., a job interview), foot tapping may carry more emotional significance than a polite smile. Unlike other non-verbal behaviors, these supposedly neutral behaviors have predominantly been explored within the framework of mimicry research, with minimal attempts to examine any potential emotional significance they might convey. We call for a more thorough examination of the underlying meanings associated with these behaviors, particularly given their extensive usage within the literature on automatic mimicry. To further advance our understanding of mimicry and its underlying mechanisms, we propose two key areas for future research. First, there is a pressing need for more comprehensive neuroimaging studies that compare different types of mimicry. Such studies may shed light on whether various forms of mimicry (e.g., facial expressions, body postures, physiological synchrony, yawning, scratching) share common neural substrates or engage distinct brain networks. This could provide valuable insights into the potential unified or diverse nature of mimicry processes at the neural level. Secondly, we call for more studies in natural contexts analogous to non-human animal behavior, particularly focusing on identifying human behavioral spheres comparable to play-fighting in primates. Play-fighting has proven to be a rich context for studying mimicry in non-human primates, offering insights into social dynamics, emotional contagion, and conflict resolution. Identifying analogous contexts in human behavior could provide a valuable bridge between human and non-human animal research, potentially revealing evolutionary continuities in mimicry functions. Such naturalistic studies in humans could complement laboratory-based research, offering a more ecologically valid understanding of mimicry's ultimate cause across species.

6. Conclusions

In conclusion, our perspective paper proposes a different function of mimicry, aiming to shed light on its evolutionary origins and adaptive significance in the past and the here and now. While previous research has predominantly focused on person-perception effects of mimicry, together with little attention to its outcomes on subsequent behavior, we advocate for a paradigm shift toward understanding its fundamental purpose. We acknowledge the selective pressures of affiliation on mimicry and agree with previous authors on the importance of social context in shaping mimicry behaviors. However, we challenge the prevailing assumption that mimicry is primarily driven by affiliative goals or positive outcome (Hess and Fischer, 2022; Lakin et al., 2003). Through a review of studies on negative and context-specific mimicry in humans and non-human animals, we showed that mimicry is not exclusively tied to positive expressions or an affiliative goal. Rather, the function of mimicry – much like emotional expressions in general (Curtis et al., 2011; Susskind et al., 2008) – should entail a foremost benefit to the mimicker. We propose that mimicry serves as a bottom-up mechanism that minimizes the prediction error, thus facilitating the prediction of the behavior of conspecifics and consequently of the environment. In this view, mimicry enhances individual survival and well-being by enabling individuals to navigate their surroundings more effectively, whether through avoiding potential harm or optimizing social interactions. While affiliation may arise as a secondary effect of mimicry, we suggest that its primary function lies in enhancing predictability and self-preservation. As we continue to explore mimicry across species and contexts, this perspective invites new avenues for investigating the broader ecological and adaptive roles of mimicry. Embracing mimicry as a mechanism for self-preservation and environmental prediction, we pave the way for a deeper understanding of social behavior and adaptation in diverse ecological landscapes.

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Declaration of Competing Interest

The authors declare no conflict of interest.

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