



Review

The body talks: Sensorimotor communication and its brain and kinematic signatures

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Abstract

Human communication is a traditional topic of research in many disciplines such as psychology, linguistics and philosophy, all of which mainly focused on language, gestures and deictics. However, these do not constitute the sole channels of communication, especially during online social interaction, where instead an additional critical role may be played by *sensorimotor communication* (SMC). SMC refers here to (often subtle) communicative signals embedded within pragmatic actions – for example, a soccer player carving his body movements in ways that inform a partner about his intention, or to feint an adversary; or the many ways we offer a glass of wine, rudely or politely. SMC is a natural form of communication that does not require any prior convention or any specific code. It amounts to the continuous and flexible exchange of bodily signals, with or without awareness, to enhance coordination success; and it is versatile, as sensorimotor signals can be embedded within every action. SMC is at the center of recent interest in neuroscience, cognitive psychology, human–robot interaction and experimental semiotics; yet, we still lack a coherent and comprehensive synthesis to account for its multifaceted nature. Some fundamental questions remain open, such as which interactive scenarios promote or do not promote SMC, what aspects of social interaction can be properly called communicative and which ones entail a mere transfer of information, and how many forms of SMC exist and what we know (or still don't know) about them from an empirical viewpoint. The present work brings together all these separate strands of research within a unified overarching, multidisciplinary framework for SMC, which combines evidence from kinematic studies of human–human interaction and computational modeling of social exchanges.

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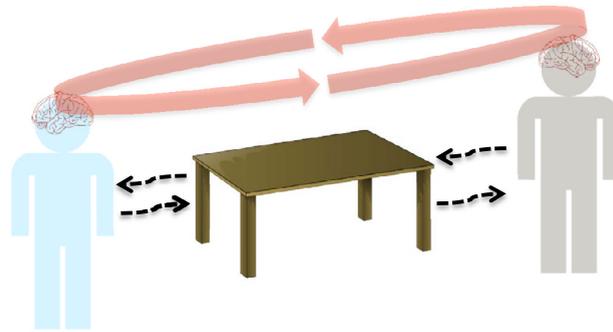


Fig. 1. A simple interactive scenario promoting sensorimotor communication (SMC). Two co-actors moving together a table are coupled both behaviorally and neurally, as their actions have reciprocal influences on the others' actions and perceptions. The red edges exemplify the fact that the brain of an agent engaged in a joint lifting task processes information about one's own and another's (or joint) table lifting. Co-actors can engage in SMC by exploiting, for example, the haptic information channel (black dotted lines) – the fact that forces produced by one agent are sensed by the other agent. For example, an agent can push the table in one specific direction (possibly, strongly) to both place the table in a desired position and also inform the co-actor of where he intends to place the table. This scenario emphasizes the fact that SMC is a combination of a pragmatic action (move the table to desired location) and a communicative action (inform the co-actor about desired table location). (For interpretation of the colors in the figure(s), the reader is referred to the web version of this article.)

1. Introduction

Across the last decades, human communication has been a flourishing field of research in many disciplines, including psychology, neuroscience, and linguistics. However, the study of human communication has principally focused on language use, gesture, and deictics. These are certainly important forms of human communication – but are they the only ones?

Evidence is accumulating that during on-line social interactions humans often use non-verbal, *sensorimotor* forms of communication to send coordination signals, i.e., signals that are embedded within standard pragmatic actions and (potentially) improve coordination success; see Section 2 for a more detailed definition. *Sensorimotor communication (SMC)* can be found in every type of social interaction – from freeform interactions like transporting together a heavy object to more ritualized interactions such as playing together in an orchestra or engaging in a dialogue. For example, a person who is transporting a table together with a co-actor can push the table in a certain direction to *signal* where and when he intends to place it. In other words, he uses a *haptic channel* rather than language to communicate (see Fig. 1). Two persons walking (or playing music) together can mark their movements to provide reference signals and a pace for coordination. When playing football, an athlete can modify his body kinematics to communicate his intentions to his teammates (say, a pass to the right) or to feint an adversary – which also reveals the fact that not all forms of *SMC* are beneficial for the receiver. A mother indicating an object to her children often over-emphasizes her movements to help the children understand her intentions; or she over-articulates vowels in child-directed speech (the so called *motherese*). Besides solving on-line coordination problems, we routinely use our body language to communicate many other things, such as our leadership, disappointment, or desire to engage in a relationship. Interestingly, all these and other messages can be flexibly embedded within virtually any action: think of how many ways we have to perform the same action, say handing a glass of wine to another person, if we want to express disappointment, love or deference. Other examples include our body posture during an interview or an exam, and our intonation and eye movements when we speak to a friend, an enemy, or want to hide a secret. One intriguing aspect of *SMC* is that, as opposed to other forms of communication that require sharing a code between the co-actors (e.g., a linguistic code), it does not seem to require prior knowledge or prior arrangements, but can arise also between persons that have never met before (although cultural differences may need to be taken into consideration). Another intriguing aspect of *SMC* is that it often consists of very subtle (changes of) kinematic or bodily cues – after all, offering a glass of wine with disappointment or deference is not so different at the kinematic level. Yet, despite their subtle nature, we are able to produce and read social signals in a very fast and efficient way, and to extract from them a surprising abundance of information about others' intentions (is he offering this glass to me or somebody else? is this soccer attacker trying to shoot to the left or right?), emotions and attitudes (is he happy or disappointed?), beliefs and preferences (e.g., does he like me or not?), etc. – yet the underlying mechanisms are largely unknown.

The topic of SMC has recently surfaced (or resurfaced) in several fields – neuroscience, cognitive psychology, human–robot interaction, linguistics, and experimental semiotics – reflecting the truly interdisciplinary nature of the topic. Despite this, we still lack a comprehensive theoretical synthesis of this multifaceted phenomenon. Some fundamental questions remain open such as which interactive scenarios promote or not promote SMC, and which aspects of social interaction are properly communicative and which ones entail a mere transfer of information.

This review is organized as follows. In Section 2, we will clarify the phenomenon of SMC from a conceptual viewpoint, highlighting its peculiarities compared to other (e.g., linguistic) forms of communication, while at the same time teasing it apart from forms of information exchange that emerge during social interactions but are not properly communicative. In Section 3, we will critically review the recent literature on sensorimotor interaction, highlighting the aspects that concern information exchange and communication. It will emerge from this review that 1) sensorimotor forms of communication are almost ubiquitous across social scenarios having various levels of complexity; 2) SMC takes different forms, exploits different channels (e.g., haptic or visuomotor coupling) and has different functions, depending on task characteristics and demands; 3) most current studies do not clearly separate communicative dynamics from simpler forms of information transfer. We will sum up the results of this review in Section 4, in which we will also propose an integrative framework and taxonomy of forms of SMC depending on different (temporal, informational and goal) demands of interactive tasks. In Section 5, we will discuss open interrogatives and propose a series of methodological indications for the design of future experiments that help charting the territory of SMC. Finally, we will draw our conclusions in Section 6.

2. Sensorimotor communication (SMC): conceptual foundations

During social interactions, we continuously use non-linguistic, *sensorimotor* forms of communication and exchange a myriad of bodily signals – with or without purpose or awareness. Social signals come in many varieties, from pantomimes and conventionalized gestures (e.g., pointing or conventional signs in poker) or facial expressions (e.g., fear faces) that have mainly a communicative function, to signals that are embedded within standard (pragmatic) actions, such as for example offering a glass of wine in a rude or polite way, or closing a window gently versus shutting it. Given the large variety of possible social signals, it is important at this stage to precisely specify what we intend by SMC. Our working definition of a SMC is *a signal that has a dual nature, and which combines a pragmatic action* (e.g., offering the glass) *and a communicative action* (e.g., express politeness). This definition teases SMC apart from (1) other forms of information exchange that are not strictly speaking communicative and from (2) other forms of communication that are either linguistic or nonlinguistic but more conventionalized and deprived or pragmatic aspects (e.g., pointing, gesture, facial expressions), see Fig. 2. In the rest of this section, we elaborate on these two distinctions in more detail.

2.1. Distinguishing sensorimotor communication (SMC) from information transfer (IT)

From a conceptual viewpoint, sensorimotor coupling in space and time between two (or more) agents – for example when they are transporting a table together – opens a communication channel (in this case, for example, a haptic channel) in the sense that – minimally – the actions performed by one agent can be sensed by the other agent (in semiotic jargon, they are *signs* or traces of events/behavior, cf. Peirce [86]), see Fig. 1. However, in communication theory and semiotics there is a distinction between these simple forms of information transfer (IT) and true communication [5,21,86]. In true communication, signs are not accidental but have the purpose to be read by somebody; either because the performer has a true communicative intention towards the addressee (e.g., wants to let him know something), or because the sign was selected by evolution to play a communicative function. As an example of the latter, in biology, one can find a variety of signals that are specialized for communicative purposes; one example is the jump of a gazelle, which is considered to be communicative in the sense that it was evolved to be read by mates and/or enemies and it communicates the animal's fitness [77]. However, not all signs that are ready by somebody else are considered to be communicative. For example, a running gazelle leaves traces on the ground, but these should be hardly considered as messages to (selected to be read by) a lion chasing it.

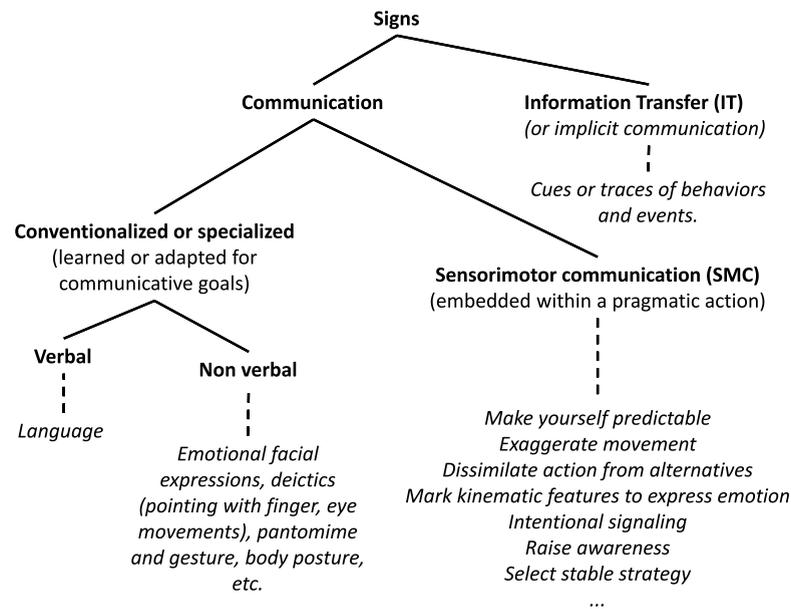


Fig. 2. **A taxonomy of signs.** Online social interaction opens information channels between co-actors – in the sense that it almost inevitably entails some information transfer (IT) between co-actors (which, e.g., can see each other’s actions). However, IT is not automatically communicative in the sense used in communication theory. It is only in some cases that agents exploit the information channel to influence or bias the information received by their co-actors (e.g., they can modify their behavior to convey some message to their co-actors), thus engaging in proper forms of communication. Therefore, a first distinction in this figure is between explicit forms of communication, which follow the prescriptions of communication theory and semiotics, and other forms of information exchange that would not count as properly communicative in communication theory, or alternatively can be considered weaker (or implicit) forms of communication. A second relevant distinction is between various forms of communication, linguistic and not linguistic – the latter including SMC. The taxonomy clarifies that we consider SMC to be a combination of a pragmatic and a communicative or epistemic action – thus distinguishing SMC from conventional forms of communication that lack pragmatic aspects, deictics (e.g., pointing) or pantomime. See the main text for additional details.

In this review, we will not cover these sort of animal signals and evolutionary adaptations, which are widely studied in the animal communication literature [110]. Instead, we will cover cases in which SMC has cooperative benefits during on-line interactions, as opposed to long-term or evolutionary advantages. Indeed, there is much more in communication than evolutionarily selected signals; for example, an animal who modifies its default behavior to alert or deceive another animal – for example, a chimpanzee approaching a food location from an angle that hides his behavior from possible competitors – [49,50,60] – could be plausibly engaging in truly communicative behavior. As the review below will show, humans exploit a variety of signaling techniques to improve interactive success, such as for example during joint lifting and transporting a table (see Fig. 1).

In sum, this short summary of semiotic theory has highlighted that true communication is not just a unilateral interpretation of a sign (as in the lion and gazelle example above), but it requires a finalized form of “sending” (or “hiding”, as in the chimpanzee example). This leaves us with a potential problem: sometimes it may be difficult to understand whether or not a behavior is communicative in this strong sense. This is why, in cognitive science non-behavioral criteria are also used; for example, it is often assumed that the *sender* has to have a *communicative intention* when leaving a sign [114]. In this vein, we can define SMC as conveying communicative messages through one’s actions, using the same sensorimotor information channel that supports a social interaction (e.g., the haptic channel of joint table lifting in Fig. 1) – essentially, by shaping the statistics of a co-actor’s inputs in informative ways. This definition is coherent with the semantics of communication in other domains (e.g., linguistics). It clarifies that SMC ultimately supports communicative goals (e.g., the goal to reduce the co-actor’s uncertainty about what to do next) and implies information shaping over and above the mere fact that interacting agents mutually sense and influence each other. It is in this sense that Fig. 2 distinguished between explicit communication (of the kind prescribed by communication theory and semiotics) from various forms of transfer of information that can be considered communicative only in an “implicit” sense (because they lack an explicit communicative intention), or even not communicative at all, if one applies the above criteria strictly.

2.2. Distinguishing SMC from other forms of nonverbal communication

Another relevant distinction, highlighted in Fig. 2, is between SMC and conventionalized or highly specialized forms of (verbal or nonverbal) communication. Conventionalized forms are those that require a learned code, such as for example language use. Specialized forms are those that have pure (or predominant) communicative functions, such as deictic gestures (e.g., pointing with a finger) or pantomime. These can be teased apart from SMC such that in SMC the signal is embedded within a standard pragmatic action that retains its pragmatic goal, e.g., handing a cup of coffee to somebody with vigor to express disappointment. In other words, we consider SMC to consist in a combination of a pragmatic and a communicative action embedded within it (say, push a table in a certain way both *to move it* and *to inform you* about where I want to move it) and it can be teased apart from other forms of nonverbal communication that lack a pragmatic aspect.

It is also worth distinguishing SMC from a variety of other signals that have biological significance such as for example innate facial expressions (expressing e.g., fear or disappointment). In addition to lacking an immediate pragmatic aspect, this sort of signal is typically fixed or stereotyped; this contrasts with the open-endedness of SMC, which can be expressed using virtually any action, as in the examples of signaling when transporting a table together or when playing football. Of note, it is this sort of open-endedness that makes SMC flexible and well suited for the demands of fast, on-line social interactions (cooperative or competitive). If one imagines two football players who have to plan an attack, it is easy to see that language or other conventional forms of communication such as pointing may be slow or inappropriate and thus SMC can play an important role in facilitating the joint plan. Another strength of SMC is that it can be considered to be a natural way to interact and communicate, in the sense that it is easily readable without prior conventions, as opposed to more conventionalized forms of communication like language that require learning a specific code. For example, the intention to place a table in a give position can be read from a partner's action kinematics.

In sum, the taxonomy of Fig. 2 clarifies that SMC has to be distinguished from both information transfer and other forms of sensorimotor communication such as conventionalized gestures. Identifying SMC as a specific category of sign is a fundamental prerequisite for its analysis during situated interactions, see below. At the same time, while the taxonomy shows strict dichotomies, some forms of SMC lie along a continuum (and can coexist) with other forms of communication; and it does not permit to fully appreciate the dual nature of SMC – and the fact that it combines a pragmatic and a communicative action. Indeed, SMC is a multifaceted phenomenon that takes different forms depending on the specific interactive situation. Below we review a number of empirical studies that illustrate in more detail what SMC is and how it emerges across various social interaction scenarios.

3. Sensorimotor communication (SMC) across various social interaction scenarios

In the previous section, we have sketched a conceptual framework that defines SMC and its differences from information transfer and other (verbal and nonverbal) forms of communication. With this framework in mind, in this Section we review empirical studies of sensorimotor interaction of various kinds, e.g., those that involve symmetric or complementary tasks, symmetric or complementary information. For each social interaction scenario, we will highlight the presence of sensorimotor communication (SMC) and the various forms it takes – also disentangling SMC from information transfer (IT) dynamics. This will not be always possible, because – as it will emerge from this review – there is a paucity of studies that explicitly control for the communicative (or not communicative) nature of interaction across almost all the interactive scenarios that we consider.

3.1. Symmetric or parallel tasks

Consider one of the simplest forms of social interaction: the case of two persons who execute the same (or similar) actions in parallel – for example, walk or play drums side-by-side – with or without joint goals. This is a fairly simple scenario, yet it offers noteworthy opportunities for sending social signals, because (at minimum) the output of an action performed by one of the actors can be sensed by, and influence, the co-actor – hence there is a possible communication channel to exploit.

A large body of literature has investigated how dyads achieve interpersonal sensorimotor (non-verbal) coordination in partially independent tasks, such as walking side-by-side [121], swinging pendulums [108], coordinating finger

movements [83], lifting from each others' trays [94] and rocking next to each other [101]. Much of this literature has taken a dynamical systems perspective, treating the dyad as an inseparable unit, showing that coordination is an emergent phenomenon that can be modeled as a system of two coupled oscillators [109] – much in the same way as other coupled systems, such as pendulums [9], fire-flies, crickets, etc. [116]. From this perspective, basic forms of social coordination, alignment and synchronization are not qualitatively different from other physical or biological phenomena and do not necessarily depend on mental constructs. These interactive dynamics are better described in terms of IT than SMC: co-actors might continuously influence each other because their actions produce (as byproducts) “signals” that are sensed by others, in much the same way the movements of a pendulum can be sensed by another pendulum coupled to it. This view would not require any form of intentional communication or even awareness. In keeping, an interesting result of this body of research is that people coordinate their actions accurately in the absence of verbal communication, and this often happens unintentionally, as they are unaware that they are influencing each other. This has led to the proposal that some sort of synchronization, mirroring or mimicking of behavior might be an almost unavoidable byproduct of interaction dynamics [63].

The dynamical systems perspective co-exists with other approaches that consider behavioral synchronization to co-exist with a range of other interactive mechanisms, which also include mental constructs including predictive mechanisms (e.g., forward models) and mental models of the current task [111]. This cognitive perspective on the architecture of interaction starts from the premise that co-actors do not simply interact with or observe one another, but also continuously predict one another – for example, by internally simulating another's actions using one's own action repertoire [58] – and form joint plans [57,96,112]. Hence, compared to a dynamical system perspective, this cognitive perspective emphasizes the importance of mental states and permits to study synchronization and alignment phenomena beyond the behavior; for example, the *interactive alignment* of cognitive representations such as beliefs and linguistic forms in dialogue [98,105]. From this perspective, apparently demanding tasks such as dialogue are facilitated because dyads tend to align their internal representations, similar to the forms of behavioral alignment and synchronization described above; this would be the case, for example, of two mutually predicting agents who align their internal models and achieve a kind of (generalized) synchrony [39,64,88]. The importance of mutual prediction – and interpersonal predictive coding – was further convincingly demonstrated by a series of studies showing that when two agents are engaged in meaningful interactions, the communicative gestures of one of the agents can provide information about and permit to predict the other agent's actions [74,75].

Importantly for our analysis, the aforementioned mechanisms of mutual prediction, mutual alignment and generalized synchrony set the stages for using SMC (although they do not automatically entail it). For example, by knowing that you are predicting me, I could intentionally shape my behavior in ways that help or hinder your predictions, e.g., make them easier to predict or align with [90,89]. For example, when two persons walk side-by-side, one of them can accelerate or slow down as a message to the other person that one likes or dislikes walking side-by-side (but note that this example implies some form of goal about the other person; this is a theme that we will come back below). However, none of the studies reviewed above (or other, to the best of our knowledge) systematically tested the presence of SMC in symmetric or parallel tasks such as the ones discussed here. It thus remains to be established whether these rather simple interactive scenarios require or allow for SMC.

3.2. *Freeform interactions*

Consider now a slightly more complex interaction scenario, in which two agents do not simply act side-by-side, but need to explicitly consider the other's action in order to plan the most appropriate response, such as for example when two musicians play or improvise a piece together. They can do it in both a freeform (or equalitarian) way, or by taking explicitly assigned roles of “leader” vs. “follower” – where the follower's action must be informed by decisions taken by the leader. These scenarios have been often conceptualized in terms of mutual adaptation and prediction, in keeping with the cognitive perspective discussed above. This second scenario could afford various forms of SMC.

One example comes from the study by Noy and colleagues [82], who investigated how people produce improvised motion together, much in the same way as in theater or music. By asking expert improvisers (actors and musicians) to imitate each other by producing synchronized and interesting sinusoidal-like motion together, they showed that people were more synchronized when engaging in joint improvisation, without reducing the complexity of motion, than when one was designated as the leader and the other as a follower. The study revealed that mutually interactive improvisation required people to both react (adapt) to one another as well as predict their partner's movements. In

particular, achieving successful motion improvisation was enabled by an interpersonal symmetric/mutual strategy. Improvisers also converged on a universal stroke of motion when jointly interacting, despite producing very different individual signatures of motion when leading an interaction [53]. One possible interpretation of this finding is that this universal motion signature was easier to predict, and hence coordination success was based on a form of SMC that consists in “being predictable”.

Similar findings have been shown in symmetric finger-tapping tasks, in which dyads have to achieve synchronization in either leader-follower interactions (where one has to follow another) or mutually interactive ones [67]. This study showed that when the interaction was bidirectional, such that each person had real-time auditory feedback of their partner’s tapping, dyads achieved coordination by mutually predicting their partner’s future tap based on their previous inter-tap interval, and adapting accordingly – if one went faster on the previous tap, the other would speed up on the subsequent one, while the one would simultaneously slow down. In other words, they did not take on the role of a leader and a follower, but of two mutually adaptive partners. Interestingly, they were as successful at synchronizing with a predictable metronome as with a less predictable partner, provided that the partner was adaptive (i.e., adjusted its tapping depending on the on-line feedback). Rather, dyads performed worse when the co-actor was both unpredictable and unresponsive (e.g., did not adapt). This finding suggests that the SMC strategy of “being predictable” is not mandatory but could act in concert with more automatic mechanisms of mutual prediction and mutual adaptation. When two partners are able to efficiently predict and/or rapidly adapt to one another, there is no need to use SMC (and not even to take leader-follower roles). When, instead, mutual adaptation is lacking, being predictable is sufficient to increase synchronization.

All of the above studies have looked at scenarios in which interacting partners had continuous (or intermittent) feedback from their partner, and hence had access to a history of their partner’s behavior with which they could predict their future actions. But what happens if such feedback is not available? A study by Vesper et al. [125] showed that when people were asked to synchronize their discrete button presses in a reaction time task, they *reduced their variability* – hence implicitly increasing their predictability – compared to when they produced a simple reaction time task alone. Importantly, the less variable they were, the more coordinated, which is coherent with the previous discussion on the benefits of the SMC strategy of being predictable. Interestingly, a similar pattern of results, with a marked decrease of motor variability, was observed in a monkey joint action study, too [129]. A similar result was also shown in a task where two participants had to build together a tower made with cubes, by using a turn taking strategy, and alternating their leader-follower roles across trials. Here, instead of measuring the temporal aspects of coordination and predictions, the analyses focused on whole arm reaching kinematics [26]. The arm velocity profile, which is a quite stable signature of ballistic arm reaching movements [79], showed higher autocorrelation in the leader, suggesting that he was trying to reduce the variability of his whole arm control in order to make himself more predictable. A follow-up research on the same data, with analyses of head and arm motion, showed dissociable effects within and between trials, and thus suggesting the existence of different cues at multiple levels [23]. This suggests that when people have no information about their partner, and are thus unable to make informed predictions, they make their own actions predictable, hence implicitly helping another’s predictions (see the Discussion).

In sum, the evidence reviewed here supports the idea that dyads engaged in sensorimotor interactions use predictive mechanisms in parallel with more automatic adaptation/synchronization mechanisms [88,93,111,120,122]. Predictive dynamics offers interesting opportunities to communicate: an agent can send coordination signals that *help another’s predictions*, for example, by reducing the variability of their actions and making them more predictable, or by modulating other parameters of movement such as its duration [93,127,128]. One can also discuss the previous findings from a complementary perspective that emphasizes feedback control rather than prediction. In this perspective, the “signals” that co-actors offer to one another are not meant to be predicted, but to be used by the co-actor as reference or set points for his own movement. Consider the example of two drummers playing together. One of the drummers might intentionally emphasize some rhythmic aspects of his piece (e.g., the beat) as a form of message to the other drummer – to give him a set point for his drumming movements. Independent of the fact that one emphasizes prediction of feedback control architectures, all these examples show that interacting partners can shape the messages they send in informative ways, thus suggesting truly communicative dynamics. At the same time, these studies suggest that SMC may not be mandatory during freeform interactions, but only manifest when mutual prediction or mutual adaptation would be insufficient.

3.3. Tasks requiring complementary roles

Consider now another scenario in which co-actors engage in joint tasks, but they have distinct and complementary roles in it. For example, two persons maneuvering a catamaran together on a windy day – one can move to the left side to keep it balanced, while another can take care of the sail. This is a typical situation in which two or more agents act together but perform different (and often complementary) actions.

One way to induce complementary action patterns is by designing tasks that have asymmetric demands. In these cases, stable coordination patterns may be perturbed, and may require people to explicitly adopt complementary strategies to compensate for these perturbations. For example, Skewes et al. [113] investigated coordination strategies when people were asked to produce synchronized clicks but had asymmetric task demands. Dyads were asked to synchronize their clicks between targets by clicking the target as accurately as possible, while task demands were changed for one member of the dyad – such that one person had a more difficult task, achieved by giving them smaller targets to click on. When dyads had similar task constraints, they mutually adapted to each other's inter-click intervals (similar to Konvalinka et al. [67]), but when their task constraints largely differed, the person with the difficult task adapted less to their partner, becoming the “leader”, while their partner (“follower”) took care of the coordination and adapted more. Since they were not aware of their partner's task constraints, this suggested that partners implicitly negotiated leader-follower dynamics with changing task asymmetries. In addition, this proved to be beneficial strategy, as they synchronized better when performing the task jointly than when synchronizing to a completely predictable metronome.

Studies on dyadic force production show that complementary strategies can also emerge spontaneously when partners have to do the exact same task. A study by Reed et al. [100] showed that haptically coupled dyads, in which their motions were physically linked, perform better (i.e. faster, as per instructions) on a target acquisition task than individuals. They do so by adopting an implicit complementary strategy, in which one participant controls the acceleration, and the other the deceleration. Interestingly, they are not aware of this, and even perceive their partner's actions as an impediment. Similarly, a study by Masumoto and Inui [76] showed that when dyads were asked to produce periodic forces such that the sum of their forces reached a target force, they adopted a complementary strategy of force production. They did so by compensating for each other's force errors – if one produced a large force, the other produced a smaller one, and vice versa, in order to reach the target force. They were also more accurate and less variable when doing the task jointly than individually.

Taken together, these studies show that adopting a complementary strategy (or *strategy flexibility*) can facilitate coordination. Is adopting a strategy a form of SMC or not? There are two (not necessarily mutually exclusive) possibilities. First, from a dynamical systems perspective, strategy flexibility may emerge as a stable solution to interactive problems, where two complementary strategies can afford better coordination than two identical strategies – in the sense that an agent's strategy automatically produces output signals that the co-actor can exploit to select his own strategy [59]. In this perspective, the selection of two complementary strategies would be a byproduct of self-organization dynamics during social interaction, not a deliberate choice. Alternatively, one can assume that adopting a given strategy might be a sort of message to the other person (“I do this part, you do the other part” or “I want to be the leader” or “I want that you adapt more to my actions”) rather than an automatic byproduct of interaction – and this second interpretation is compatible with SMC. Current evidence cannot easily adjudicate between these (or alternative) possibilities.

However, there is at least one case in which strategy flexibility does not seem to require SMC. Vesper et al. [124] investigated coordination strategies in an asymmetric task by asking dyads to coordinate jumping actions by landing in temporal synchrony. However, they were given different distances to jump, such that one person had a larger distance to cover. While they could not see their partner, they were made aware of their partner's jumping distance prior to each trial. The authors showed that dyads overcame this asymmetry by adopting a complementary strategy – the person with the shorter jump adapted their actions to their partner's task demands by waiting longer before jumping, while the person with the longer jump adapted less. Importantly, in this experiment participants were not actually able to see or sense other's actions (they had no obvious communication channel during action planning), thus preventing forms of on-line sensorimotor communication. In these cases, subjects might infer coordination success by *predicting* another's strategy. This more demanding form of coordination based on predicted strategies might be similar to the idea of *focal points* in team reasoning [106,117] – where essentially one asks what the other agent would optimally do based on salient shared knowledge (e.g., when two tourists in Paris both decide to meet under the Eiffel tower, without

making prior arrangements). Interaction success may reinforce the common knowledge and ultimately the selected strategies (i.e., “this strategy was successful, let’s keep using it”) without explicitly requiring communication.

In sum, this body of literature suggests that role allocation and negotiation can occur automatically and without SMC, although in some cases SMC could be employed. In other words, the necessity to take complementary roles is not a sufficient condition for SMC. It is possible that SMC becomes more important in tasks that are more complex than the ones reviewed here, such as for example tasks that involve repeated interactions to solve long-term goals (e.g., when two persons have to split roles when cleaning a table together) but this hypothesis remains to be tested in future studies.

3.4. Joint tasks with asymmetric information

Imagine now another scenario, in which two agents have to coordinate their actions to achieve a common goal (say, moving a table together or composing together a mosaic) but have asymmetric information (say, only one of the two partners knows where the table has to be moved or which mosaic should be done). This is an ideal condition to promote communication – and this is where SMC has been explicitly tested in a number of studies.

For example, Sacheli et al. [102] have tested a leader (with full task information) and a follower (with incomplete information) in a joint task consisting in grasping together a bottle that could be grasped in two different places (upward or downward) – where only the leader knew the correct grasping location. The study shows that the leader carves his action kinematics to make his actions more readable and its intentions easier to understand by the follower. For example, the leader can signal his intention to execute an upward movement by raising his arm much sooner compared to control conditions in which the follower has full information.

This result parallels evidence in other fields, (e.g., motherese and motionese) that mothers amplify or exaggerate vowels (or arm movements) when talking (or gesturing) to their child – possibly, to help the child to extract and learn multimodal contingencies [69]. However, the aforementioned study shows that SMC is not limited to a pedagogical (mother-child) context but is a more general interactive mechanism. Most intriguingly, a computational analysis and modeling of the experimental study reported by Sacheli et al. [102] has shown that the changes in movement kinematics are more than just “exaggerations” of movement: they are attempts to dissimulate or disambiguate the selected action (upward) from the alternatives (downward) [90]. Given that in this framework the “message” has a specific content (say, signal that I am doing action A and not B) and it is not a generic mechanism to raise the follower’s attention on my action, it has been called a form of “signaling”. A prediction of this framework is that the leader should modify its action kinematics (“signal”) in different ways depending on the choice alternatives, not just exaggerate the selected action in a stereotypical way. This prediction has been confirmed by the results of another study [123], in which a leader and a follower were asked to press (simultaneously) one of four possible buttons – and only the leader knew which one. The results show that leaders modified their button-reaching movement kinematics (signaled) differently depending on which was the correct buttons to press; in other words, they were able to embed a specific communicative message (“press the third button” or “press the fourth button”) in their movement kinematics. Taken together, these two experiments indicate that signaling is a flexible form of SMC that can convey a specific message, to resolve the follower’s task uncertainty. Of note, the Vesper and Richardson [123] study also shows that SMC and more automatic mechanisms of behavioral coupling are not mutually exclusive but can coexist in the same task.

Two other studies ask explicitly whether or not this form of SMC is intentional (or strategic) – where intentional does not mean conscious, but the result of strategic cost-benefit computations rather than an automatic byproduct of interaction dynamics. Candidi et al. [11] designed a follow-up of the Sacheli et al. [102] experiment, in which leaders and followers interacted repeatedly over many trials. Unknown to the follower, the leader’s actions followed some regularities or “rules” (say, the triplet “up, down, up”). The study shows that leaders usually stop sending coordination signals when (he infers that) the follower has implicitly understood the rule – which is a hallmark of a flexible strategy. Along similar lines, a study of sensorimotor “signaling games” has shown that SMC decreases with increasing signaling costs and decreasing uncertainty of the follower [71] – which is again an index of a flexible (cost-benefit) strategy. Pezzulo and Dindo [93] designed a task in which two agents, leader and follower, had to jointly build a tower made of bricks of different colors; but only the leader knew the tower design. Similar to Candidi et al. [11], the authors found that leaders considered the follower’s uncertainty about the tower design when deciding whether or not engage in SMC – and in particular, they stopped sending coordination signals when the follower resolved his uncertainty. Among the other things, this study suggests that not only SMC can be used in the short

run to inform a co-actor about one's own actions, but also in the long run to *align task representations* [112] and form *common ground* with him [21]. In turn, when there is sufficient common ground, there is no need for more communication – which is exactly what theories of communication prescribe [47] – because dyads using a common ground produce a coordinated sequence of actions and predictions [92].

Taken together, these studies highlight that asymmetry of information between interacting co-actors makes SMC necessary or at least very useful. The studies we have reviewed emphasized a form of “signaling” in which leaders shape their action dynamics in ways that are informative for the followers. Furthermore, they revealed that this strategy is flexible and is only (or preferentially) used when followers are more uncertain. This flexibility can be modeled by appealing to a form of cost-benefit computation, which weighs the costs of signaling (e.g., the biomechanical costs necessary to execute an uncommon action) against its benefits for the follower (e.g., in terms of increased action understanding or information gain) and ultimately for the dyad. It is also worth noticing that even though this form of signaling often consists in rather minimal changes in the parameters of action execution (i.e. joint configuration or velocity profiles), they are read appropriately by followers. This is in keeping with studies showing that humans are able to read others' actions and goals from early kinematic cues elicited during movement [3,104]. This is important because it offers the opportunity to use subtle kinematic changes of one's own action patterns as a very flexible code for SMC in ecological interactions, as we review below. This is also important from a methodological perspective, since the detailed analysis of kinematic patterns is proving to be a valid methodology to understand human social interaction in its full complexity, offering a valid vantage point to decode the co-actors' intentions [2,8,68].

3.5. SMC in ecological interactions

So far, we have focused on rather simple cases of social interactions. However, one pressing question is whether the mechanisms of SMC elucidated in these simpler scenarios are also in play in more ecological cases, such as for example when we meet a person we love or hate, when we face an opponent before a boxing match, or during a job interview. Unfortunately, behavioral experiments investigating SMC rarely implement the ecological complexity of natural interaction. However, recent studies have begun to address the complexity of real-life interactions; for example, by measuring (unobtrusively) motion kinematics from small groups embedded in ecological social interaction to extract continuous information flow from participants.

One appealing way to address ecologically valid interactions and SMC is by studying ensemble musicians [26,61,62,73,130] and their non-verbal exchanges across several information channels e.g., technical/instrumental (i.e. piano fingering) or ancillary movements (i.e. body sway), which are not directly necessarily for sound production. Empirical studies of ensemble musicians have revealed that the same mixture of social coordination mechanisms we discussed in relation to laboratory experiments – which include forms of information transfer, synchronization and prediction, as well as SMC – can be found also in more ecologically valid contexts.

One line of research in this domain indirectly studied SMC by asking how individual behavior changes when it is part of a joint action or not. This research line has shown that pianists, when playing with someone else, adjust their timing patterns regardless of whether they are playing the melody or the accompaniment [45], see also [16]. Another study revealed that all players engage in phase correction, but the leader in a quartet, corrects less strongly than the others; and different quartets have different internal social structures, which can be revealed by the different patterns of adjustment between players [131]. Such successful coordination is heavily based upon prior knowledge. Familiarity with the co-performer affects the coordination of keystrokes in piano duos, while knowledge about musical structure influences coordination at the level of body sway [99]. Another set of studies analyzed the expressive ancillary movement of quartets playing in solo and in ensemble, showing higher predictability of head movement in the joint action scenario [44]. A similar question motivated another study that analyzed technical movements (bowing) as well as audio recordings of quartets [84], showing that dynamical group interaction may be based on sharing information along multiple levels (intonation, dynamics, timbre, tempo), each potentially characterized by different temporal scales. The results of these studies – and the difference between solo and joint conditions – suggest that co-actors shape their behavior in informative ways, thus engaging in forms of SMC. However, these studies have not been designed to test SMC or to study its efficacy in terms of increased interaction success, hence this conclusion remains tentative [17]. While these studies reveal important coordination and synchronization dynamics that are similar to those reviewed above during freeform interaction, they do not clarify whether they are due to forms of information transfer between co-actors or SMC.

A study that addressed SMC more directly was conducted on quartets' ancillary movements, applying temporal and dynamical changes to the musical score, which were known by the first violin only. This manipulation was devised to generate an artificial informational asymmetry between participants, and force unidirectional communication from the first violin. Global group coordination was increased while the first violin reduced his influence towards the rest of the group [7]. This showed that the flexibility in establishing novel complementary strategies was no longer possible with expert musicians. Here we must consider that in highly skilled individuals, joint action coordination is based on thousands of hours of joint rehearsal, potentially leaving limited space for large behavioral flexibility. At present, it is still an open question whether the increase in joint action expertise is directly associated with a reduction in the flexibility by which participants mutually implement complementary strategies or use SMC. Instead, it is possible that expertise instead allows greater flexibility, but at different timescales.

A complementary line of research has studied SMC at the global (i.e., whole orchestra) level. One study investigated whether network fluctuations of causal relationships among orchestra players were associated with the aesthetic quality of the musical execution, showing that the increase of conductor-to-musicians influence – plausibly supported by SMC mechanisms – together with the reduction of musician-to-musician coordination, is linked to quality of execution, as assessed by musical experts' judgments [25]. This study shows that the analysis of motor behavior provides a tool to investigate the SMC dynamics of small groups (instead of merely dyads) when working together toward a shared goal. More broadly, this line of research prompts questions about the possibility for SMC to play functional roles in addition to increasing task performance; for example, whether synchronized group behavior can effectively signal something to perceivers outside the group – to an audience. This question has been investigated in a study of synchronized behavior in soldiers and military parades [37]. This study shows that participants judge teams of synchronized soldiers to be larger and more effective, suggesting that SMC can play a functional role outside the group (e.g., scare opponents) in addition to a role within the group (e.g., enhance social bonding). Here, in other words, the behavior of a military group can signal something to an external audience (an opponent group), in the same way the group behavior of an orchestra or a ballet has communicative implications for the audience and can influence the quality of their aesthetic experience. Studying the communicative implications of within-group SMC for an external audience is an interesting topic for future research.

In sum, the studies mentioned here begin to shed light on mechanisms of SMC in ecological contexts. They have revealed that some of the SMC mechanisms elucidated above (e.g., subtle changes in movement kinematics to make one's movements more predictable or discriminable) are part and parcel of ecological interactions. The fact that SMC is used during performance suggests that it might improve coordination success within the group (e.g., increase synchronization); and this in turn may have additional communicative effects that extend beyond the group (e.g., improve audience experience in the case of music, or scare the adversary in the case of a military group). It is worth noting that, in this Section we have focused on music and auditory-motor coordination, in contrast to mostly visual-motor coordination reviewed in the previous Sections. There are no specific reasons to believe that the underlying mechanisms should be different, but the possible modality-specific dynamics of SMC remain to be fully assessed in future studies.

Furthermore, future studies should extend the range of ecological interaction in which SMC is tested. One interesting extension would be studying SMC in interactive contexts that, like orchestras, are partially structured, such as in team sports. However, as our examples in the introduction have suggested, SMC can be studied in less structured interactions as well, such as when dating, during an interview or an exam. In real life, there are many actions that can be used as messages, such as for example closing a door as an implicit message that one does not want company, or (for a criminal organization) firing a shop to signal power or control over the zone, see also the discussion in Castelfranchi [13], Castelfranchi et al. [12,14,15] on *behavioral implicit communication*. Studying these more complex scenarios will help extending our knowledge of the communicative dynamics that regulate our social life.

4. Summing up: charting the plurality of forms of SMC

Our review in the previous Section has highlighted that SMC is not a monolithic construct but it takes a variety of forms. We have reviewed several studies collectively showing that SMC is widespread in simple dyadic interactions [102] as well as in large-scale interactions (e.g., quartets, [7]). It can be revealed by analyses of body kinematics [123], where some specific fingerprints can be found such as the exaggeration of movement, and – as we will see in a later Section – potentially by analyses of brain mechanisms and rhythms (e.g., frontal networks in coordination

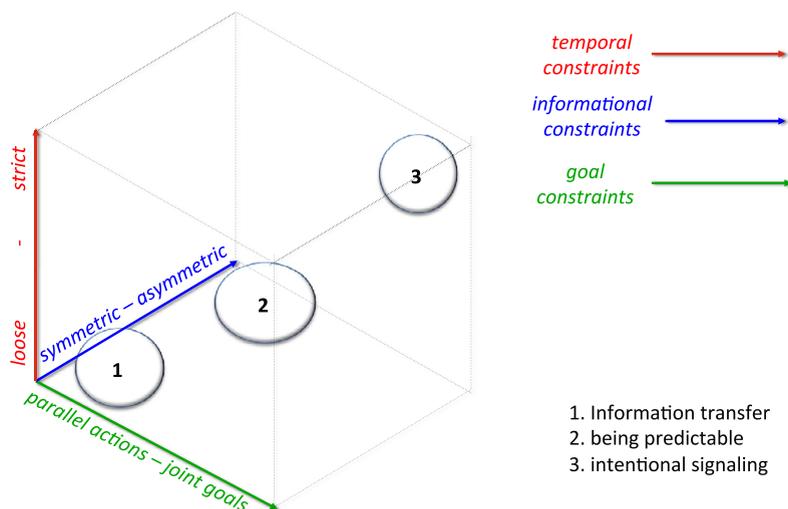


Fig. 3. **Organizing IT and various forms of SMC along temporal, informational and goal axes.** The figure synthesizes the results of our review, and shows that tasks that differ in their temporal, informational and goal demands may afford information transfer and different forms of SMC. For the sake of simplicity, in the figure we only highlight three phenomena, which correspond to 1. *information transfer* and 2. *being predictable* (i.e., a relatively simpler form of SMC) and 3. *intentional signaling* (i.e., a relatively more complex form of SMC). See the main text for clarifications.

leaders, Konvalinka et al. [65]; inter-brain synchronization, Yun et al. [134]). It is generally beneficial for interactions, e.g., it simplifies online coordination and intention recognition and improves dyad performance [11]. SMC can take different forms, depending on task demands (e.g., whether or not one of the co-actors has information that the other cannot access directly, [31,93]); and it can be interpersonally negotiated to facilitate interaction, in some cases leading to the emergence of social roles such as leader and follower [67,113]. In most studies, it has been shown to leverage on predictive mechanisms – exploiting the fact that given you are predicting me, I can guide your expectations in informative ways [82,85,90]. Taken together, our review suggests that there is a *plurality* of forms SMC can assume, as also reflected in the list of SMC of Fig. 2. While future studies are required to completely chart the territory of the possible forms of SMC, there are already many lessons to be learned from the studies we reviewed, and in particular about the most important constraints that promote or do not promote it.

As a contribution towards a better conceptualization of different forms of SMC, we propose to organize them along three main axes, which consider temporal, informational, and goal constraints of interaction, see Fig. 3. The first (temporal) axis considers how strict the time demands of the task are, such as for example whether the two co-actors have to coordinate and synchronize their actions precisely in time or not. The second (informational) axis considers whether or not information is shared between co-actors. The third (goal) axis considers the presence or absence of joint goals. These three axes correspond to the three task dimensions that, according to our previous analyses, are more crucial to determine SMC; and we can map the different forms of SMC reviewed above in the 3D space of Fig. 3.

We argue that as task constraints become stricter across one or more of these axes, they afford various forms of SMC, from simpler to more complex. When tasks have loose temporal, informational and goal constraints, they do not necessarily require SMC, hence we mark this territory in Fig. 3 as dominated by information transfer (IT) dynamics. Tasks that have strict temporal constraints but loose goal constraints (e.g., tasks involving the parallel execution of different actions) promote some weak forms of SMC in addition to information transfer. For example, participants may make their behavior more predictable to avoid collisions or mark/highlight aspects of their actions for the sake of others. With joint goals, co-actors may need to coordinate around a common strategy, or select complementary roles/strategies, and forms of SMC such as following a recognizable strategy or a predictable pattern of behavior seem useful – although it is not always easy to understand to what extent these phenomena are an emergent byproduct of interaction or explicitly communicative.

The most sophisticated forms of SMC that we have reviewed, and especially *intentional signaling* (e.g., an attempt to disambiguate one's own actions from alternatives), emerge in the presence of strict constraints on all the three axes: temporal, goal and (especially) informational. The reason why we consider *intentional signaling* more sophisticated than other forms of SMC is its flexibility and context-dependence. Strategies such as *make yourself predictable* (or

reduce the variance of your movement) seem not to be flexible: when driving, you might want to follow predictable trajectories, without necessarily caring about the mental states or uncertainty of others, and without necessarily targeting the message to different persons (hence they might also correspond to behavioral habits [29]). On the contrary, *intentional signaling* is a flexible and context dependent strategy, both because one can signal differently depending on the intended message [123] and because it is suppressed when the co-actor's uncertainty is minimized [71,90]. This strategy can be thus assumed to stem from cost-benefit considerations, in which the (informed) leader faces a trade-off between the costs of sending a coordination signal and the benefits in terms of interaction success – similar to Grice's *Maxims of communication*, which prescribe to making your contribution relevant or as informative as is required for the current purposes of the exchange [48]. Yet, the current data on SMC (including intentional signaling) do not clarify to what extent this putative cost-benefit computation is explicit, or whether the underlying communicative intention is as sophisticated as implied in communication theory and linguistics (e.g., whether it includes the intention that the addressee recognizes one's own intention to communicate [114]). These open interrogatives remain to be studied in future research.

5. Open problems for the study of SMC

Our review has elucidated various forms of SMC but also highlighted our current gaps in our understanding on this phenomenon. In this Section we discuss some open problems and current barriers to our understanding of SMC, also offering some methodological considerations on how to address the problems.

5.1. Distinguishing communication from information transfer and other forms of communication

As we discussed at the beginning of this paper, interacting opens up a communication channel between co-actors – but not all forms of interaction entail true communication. Distinguishing true examples of communication from other forms of information transfer is key to develop a theory of SMC and investigate it empirically. The taxonomy of Fig. 2 clarifies that some automatic forms of information exchange that (along with behavioral alignment, synchronization, etc.) emerge as byproducts of interaction dynamics [59] might not be properly communicative in the sense used in linguistics and communication theory [114]. From this perspective, the mere fact that by executing my movements I create good cues for your movements/plans, is certainly important to enhance coordination success, but is not necessarily communicative. Alternatively, if one relaxes the criteria, some of the information exchanges that take place automatically during interactions might still be considered to be communicative, but only in a weak or implicit sense.

In our review, we have tried to clarify which experiments target directly SMC mechanisms and which ones target information exchanges that are not explicitly communicative. However, teasing apart communicative vs. non-communicative aspects of interaction dynamics is sometimes challenging, especially in realistic interactions that can elicit a combination of communicative and non-communicative exchanges. Think for example of two martial artists engaged in a fight [133]: some aspects of their movements might be required to hit the opponent, some to feint him, others might be more routinized attacks that in turn the opponent can recognize – and teasing them apart is not always simple. A second element to consider is that the taxonomy of Fig. 2 includes some simplifications and there are some mixed cases; for example, while transporting a table, one can use a mixture of specialized signs such as pointing, along with language and SMC methods such as pushing a table in a specific direction. If one considers the full complexity of ecological set-ups, it is plausible that explicit and intentional forms of SMC act in concert with more automatic mechanisms (e.g., of resonance, co-adaptation, synchronization and imitation) giving rise to rich interaction dynamics, which include interesting communicative aspects. In keeping, one of the studies reviewed above finds evidence for a combined role of automatic and strategic forms of signaling during a joint task with asymmetric information [123].

Methodologically, future studies would need to explicitly probe whether agents who use SMC indeed have communicative intentions – which would be a key prerequisite for true communication in semiotics and communication theory – and whether their co-actors recognize these communicative intentions. While this is not always simple, a signature of intentional communication (as opposed to mere information transfer) seems to be its flexibility – for example, the fact that it appears only in interactive scenarios (as opposed to solo actions) and when co-actors are uncertain, i.e., with information asymmetry. Another signature flexible SMC that remains to be fully tested is the possibility to carve own kinematics in different ways, to fulfill different communicative intentions and to convey different

messages [90]. From our review, information asymmetry and the presence of joint goals seem the most important prerequisites for sophisticated forms of SMC (see also Fig. 3), hence tasks that include them can be effectively used to chart more accurately the territory of SMC.

Another possibility to consider when designing experiments that address SMC is testing how SMC might work together with other forms of communication, linguistic or nonlinguistic. In everyday joint activities, people can use a combination of linguistic signals, SMC and material signals (signals in which they indicate things by deploying material objects, locations, or actions around them) [21,20]. Studying how these forms of communication can be flexibly combined remains an open avenue for future research.

5.2. *Assessing the role of SMC in the architecture of social interaction*

Another important research direction is understanding what is the role of SMC in the architecture of social interaction – or, what is SMC for – and what optimality principles may underlie it, e.g., which elements may guide the choice of sending or not a communicative or coordination signal during interaction.

As a contribution towards an advanced theoretical understanding of SMC, we start from the premise that SMC is an effective – yet poorly recognized – mechanism for alleviating the burden of online social coordination problems. It has often been remarked that social interaction poses huge cognitive and computational demands, for instance in terms of mutual/recursive mindreading and the parallel planning of one’s own actions and predictions or the co-actor’s movements. One problem with this view is that it describes interaction from an individualistic perspective, assigning the whole burden of (for example) prediction and action/intention recognition on the perceiver agent’s side. We propose, instead, to look at coordination problems from a more interactive perspective [42,92,112] – one in which, for example, co-actors can form joint goals and help one another using SMC; for example, a performer agent can improve the perceiver’s prediction success by making his action more predictable or more discriminable [90,125]. In this perspective, SMC can simplify social coordination problems – or act as a *coordination smoother* [126] – because it facilitates reading the kinematics and recognizing the intentions of a co-actor (in cooperative domains) – or, conversely, it can be used to feint and make body kinematics and intentions more opaque (in competitive domains). In sum, SMC may bring significant advantages for the dyad: it splits a difficult inference problem (e.g., infer another’s intention from his observable behavior) into two simpler problems, one solved by the performer agent (select a discriminable action) and one solved by the perceiver agent (infer another’s intention from his observable behavior, but once this behavior has been made discriminable and predictable).

This latter consideration suggests that there may be optimality (cost-benefit) principles underlying SMC and (for example) the choice to send or not send a coordination signal during interactions, which can be explored with the aid of recently developed computational models of interactive dynamics and joint actions [31,39,87,90,93]. A class of models that we argue to be particularly appropriate to this purpose are those based on the idea that internal generative (or forward) models underlie action production, perception and simulation [19,18,38,58]. The appeal of these models is that they connect well with a body of literature showing that both joint actions [111] and dialogue [90,92,97,96] are heavily based on predictive mechanisms and forward models [28,132]. Prediction does not necessarily entail communication but it opens the doors to efficient communication. For example, a leader can predict the possible consequences (the plausible communicative effect) of a given message, or in other words whether the message will help the follower. This idea has been explored using a computational model of intentional signaling, which showed that the decision to send or not a communicative signal can be cast as a cost-benefit computation, in which the leader trades off the costs of signaling and its benefits for the follower and ultimately the dyad [90]. Other related models have explored the possibility that SMC may have longer-term effects, such as for example aligning co-actors’ internal models, which in turn would improve interaction success and relieve agents from the burden of continuous and mutual prediction and mindreading [39,94,93]. These models have shown that when the co-actors’ generative models become aligned interaction success improves – and it is in these cases that the leader can safely stop sending coordination signals [93]. Finally, some recent examples of the potential benefits of SMC in interactive contexts come from human–robot studies. These studies show that “exaggeration” of the robot movements and signaling dynamics improve legibility of behavior [32], which might in turn entail improved coordination success, acceptability and trust [30].

Clearly, these models and related ones are just starting points and many questions remain open, including the empirical validity of the putative optimality principles and the brain correlates of the underlying computations, including for example action simulation, recipient design or shared visual information [57,80,127].

5.3. Understanding the brain mechanisms underlying sensorimotor communication

While research has investigated behavioral mechanisms underlying SMC, the underlying brain mechanisms remain poorly understood. Much of the literature has investigated individual processes in scenarios where participants are isolated from a social context, and hence isolated from a real communication with another. Only recently have researchers begun to design interactive experiments, and in particular, explore neural mechanisms of two people simultaneously as they engage in sensorimotor communication (see [6,34,66,55] for reviews). Methodologically, these interactive studies go beyond action observation setups and can address the mechanisms of interpersonal coordination and communication. Yet, there is currently a paucity of studies that address SMC directly. Despite so, some recent findings provide some hints on candidate neural signatures (e.g., specific brain rhythms) that are promising to consider in future investigations of SMC.

A dual EEG recording of interactive finger-tapping revealed one candidate neural signature. This study [119] looked at neural oscillations underlying interactive finger movements, by recording dual EEG from pairs of participants as they produced self-paced rhythmic finger movements while either able to see each other's hands or where the view of the partner was blocked. Investigation of the underlying neural oscillations revealed two components (ϕ_1 and ϕ_2) over the centro-parietal areas in the 9–12 Hz frequency range – one that was enhanced with independent movement and the other with coordinated behavior. This study suggests that self-monitoring (presumably underlying independent behavior) and monitoring of the self in relation to the other (during synchronized behavior) is modulated by 9–12 Hz neural oscillations over the sensorimotor cortex.

Many other studies have also reported amplitude modulation of oscillations around 10 Hz over the sensorimotor cortex (i.e., interpersonal coordination: Dumas et al. [33], Konvalinka et al. [65], joint attention: Lachat et al. [70]). Specifically, these studies have shown a stronger amplitude-suppression of 10 Hz oscillations during interactive behavior in contrast to non-interactive. These oscillations correspond to the rolandic mu-rhythm [43], which has also been found to suppress during execution or observation of movement in contrast to rest [10,22,95]. This suppression is thought to be indicative of activation (or release from inhibition) of the sensorimotor cortex [95]. When people engage in joint actions, they produce their own actions while simultaneously perceiving the actions of their partner. Hence, their action outputs become their partner's perceptual input, and vice-versa, coupling them via action-perception links [51]. Mu-rhythm suppression has thus been proposed to be an index of action-perception coupling [27,52] and can be an important index to study when information is transmitted through sensorimotor channels.

There has also been great interest to investigate whether there are interpersonal mechanisms on the neural level that are similar to the behavioral level – for example, neural processes that distinguish leaders and followers. Several studies have investigated this question by recording EEG simultaneously from two partners engaged in SMC. By employing brain-decoding techniques to distinguish interactive from non-interactive conditions, one study has shown complementary neural mechanisms between two partners, one a leader and the other a follower [65]. Specifically, the leaders were characterized by a suppression of right-frontal 10 Hz oscillations when leading their partner versus following a computer-generated stimulus, while there was no difference in the followers' brains when they followed another individual versus a computer stimulus. This suppression mechanism may be one of the neuronal signatures of leader-follower SMC, but future studies are required to investigate the mechanism in more detail. Another study investigating finger tapping along with an adaptable stimulus similarly found that activity in the right-frontal cortex, involved in self-processing and cognitive control, correlated with the perception of leadership [36]. Taken together, these studies suggest that right frontal brain areas are activated during planning and control – which are required by participants as they anticipate and plan to take over leadership of the task or to communicate; or alternatively as they allocate more resources to self-monitoring.

This asymmetry in leaders and followers has also been reported in studies that have quantified synchronized inter-brain effects. A study of guitar duets reported directed phase coupling from frontal electrodes of leaders' brains to those of followers', also in the alpha frequency band [103]. Similarly, directed oscillatory coupling across various frequency bands was found between two partners' brains during a more strategic card-game task – namely, prefrontal areas of a leader and ACC/parietal areas of the partner [4].

Another study investigated implicit interpersonal coordination by asking two partners, sitting face-to-face, to keep their index fingers still and directed at each other [134]. Following a training session, where one person had to follow the movements of the other (as the finger moved within a square), the participants unconsciously synchronized their fingertip movements in relation to the pre-training session, even though they were instructed to keep their fingertips

stationary. This unconscious coordination did not happen following a non-social control session. Interestingly, this coordination was associated with an increase in inter-brain synchronization in theta and beta frequency bands, and was asymmetric between the brains of those who had the role of leaders and those who had the role of followers during training sessions.

Research has also investigated neural mechanisms during more complex interpersonal movements, for example, communicative gestures. Dumas et al. [35] employed a two-person hand imitation task, asking participants to spontaneously imitate their partner's hand gestures, while recording dual EEG. Interactive trials were divided up into synchronized and non-synchronized episodes – first, not taking into account whether the movements they produced were the same, and hence imitative – and inter-brain phase-synchronization was quantified across alpha, beta, and gamma frequency bands. The authors found increased synchronization during synchronized vs. non-synchronized movements across all frequency bands, between centro-parietal and parieto-occipital areas. However, there was no difference in inter-brain effects when contrasting imitative versus non-imitative episodes, suggesting that these interpersonal effects cannot be attributed to producing the same actions, but rather to the temporal coordination of behavior.

Several studies have also reported coupled brain-to-brain effects during communicative tasks that do not involve temporal coordination. Anders et al. [1] investigated correlated activity between brains using fMRI to scan two people in a pseudo-interactive scenario – one was asked to indulge in emotional situations and facially communicate their emotion to their partner while scanned, while the other was scanned separately and played back the sender's facial expressions via a video system, and asked to merely watch their expressions and try to feel with them. The authors found that the activity in the perceiver's brain could be predicted from the activity in the corresponding network of the sender's brain at a temporal delay, which decreased over time. Similarly, another study investigating sender-receiver inter-brain interactions during a game of charades [107] – where the sender gestured words to the perceiver – found that the sender's brain signals predicted the perceivers, also at a temporal delay (senders' preceding the perceivers'), across brain areas shown to be activated during mentalizing and mirroring.

Whether these inter-brain coupling effects indeed constitute a brain mechanism underlying interpersonal coordination, or emerge as a consequence of the similarity in behavior remains unclear. One of the difficulties in devising paradigms that address two-person SMC is properly controlling for behavioral outcomes, to ensure that the effects seen are not merely driven by similarity in sensorimotor feedback. In addition, to address the question of whether inter-brain synchronization has a causal role on behavior (and is not just a byproduct of interaction dynamics), research should jointly consider synchronization in brains and behavior – where the brain-to-behavior directionality is especially informative for causality. In other words, is there a benefit to synchronizing brain signals with another, or is it trivial that this occurs in order for us to align our actions and perceptions with others? One recent study has addressed this issue of causality, and found that interpersonal coordination was enhanced when people's motor cortices were in-phase synchronized, as achieved using tACS [81], suggesting a possible function of inter-brain synchronization in social interaction. In order to fully understand neural mechanisms underlying SMC, these “brain-to-behavior-to-another's brain-to-behavior” interactions will require more careful experimental design and computational modeling to properly disentangle actions, perceptions, and joint action effects. A further methodological consideration is that – as discussed above in Fig. 3 – one should expect a range of different forms of SMC, and associated brain processes, depending on task demands. For example, brain areas that have been shown to be involved in recipient design or intention recognition [40,51,54,115] may be engaged (or aligned between co-actors) only in the most sophisticated forms of SMC. Targeting scenarios with different temporal, informational and goal demands would allow to disentangle the differential contributions of brain areas across various forms of SMC. In sum, this summary of neural studies has clarified that the brain bases of SMC remain largely to be charted, and this requires solving technical and methodological problems; however, future studies can leverage on a growing body of studies that address related questions (e.g., leader-follower interactions) and the candidate neuronal signatures that these studies have identified as relevant for interpersonal coordination.

6. Conclusions

When two or more agents interact, an information channel opens which gives them plenty of opportunities for communicating. Communication can take many forms; our discussion has focused on *sensorimotor* forms of communication (SMC) that are neither linguistic nor conventional or specialized (such as for example pointing) but seamlessly

integrated within the agents' pragmatic actions. Think for example at how many nonverbal messages one can send, or receive, during a football match, a job interview or when one is dating. Even though most of these signals are quite subtle, they seem to be fairly understandable or readable by our conspecifics: after all, we are a social species and the ability to exchange social signals might have contributed to our adaptive success.

The studies discussed above illustrate that SMC emerges across various social interaction scenarios, generally enhancing sensorimotor coordination. We have highlighted key behavioral and brain signatures of SMC across various interactive tasks, from walking side-by-side to building something together. We have discussed how to distinguish SMC from forms of information transfer (IT) that are not strictly speaking communicative, and identified how temporal, information and goal constraints promote different forms of SMC. Finally, we have identified some important open questions such as how to study the neuronal bases of SMC, and what is the place of SMC in the architecture of social interaction.

The body of research we have reviewed provides also a fresh perspective into more complex – for example, linguistic or conventionalized – forms of communication, which might partially reuse the mechanisms supporting sensorimotor communication, and whose adaptive value might be traced back to the demands of social coordination problems. In this perspective, some productive research fields such as *experimental semiotics* [41] are studying the emergence of complex forms of communication, possibly on top of simpler ones; see also a recent study on the rapid emergence of communicative conventions through simple signals in repeated interactions [78]. For example, it has been repeatedly proposed that communicative signals might have initially evolved on top of interactive patterns. One example is the case of pointing (a deictic gesture), which might derive from the pragmatic action of grasping. Another possible example is smiling (a prototypical expressive facial signal), which might have gradually evolved as a stylized human signal on top of existing (non-communicative) mechanisms to steer defensive actions [46]. These examples suggest the intriguing possibility is that some signals exchanged during sensorimotor communication may (after repeated iterations within a dyad or a team or a society) become conventionalized – and therefore part of a more stable (and less freeform) communicative repertoire. As we have emphasized, part of the appeal of these signals is that they are not just communicative but they also contribute to (joint) plan achievement; think for example to a common situation in cafeterias, where placing a saucer in front of a person is both a signal (the next coffee will be for you) and part of the pragmatic plan of serving a coffee – thus relating to the idea of *stigmergy* in animal-animal interactions [118].

Along similar lines, one can also imagine that the rich interactive dynamics of SMC that we have reviewed here scaffolded more complex forms of communication, including linguistic communication – because, essentially, the latter can reuse the rich pragmatic skill, or *interactive engine* [72,91] that is already visible in SMC. In this perspective, sensorimotor forms of communication may have gradually transformed in more conventionalized and symbolic ones, which also include a code (e.g., a linguistic code) as possibly these latter forms are more open-ended and stable. Along similar lines, one can imagine that during development, SMC might also help establishing a *pedagogical context* for social learning [24] and scaffold the acquisition of sophisticated forms of mindreading [56] and even linguistic communication [92]. The appeal of these hypotheses, which remain to be scrutinized in future research, is that they would show a clear link between communication and the adaptive benefits of social coordination [5].

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