Review

From neural noise to co-adaptability: Rethinking the multifaceted architecture of motor variability

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A B S T R A C T

In the last decade, the source and the functional meaning of motor variability have attracted considerable attention in behavioral and brain sciences. This construct classically combined different levels of description, variable internal robustness or coherence, and multifaceted operational meanings. We provide here a comprehensive review of the literature with the primary aim of building a precise lexicon that goes beyond the generic and monolithic use of motor variability. In the pars destruens of the work, we model three domains of motor variability related to peculiar computational elements that influence fluctuations in motor outputs. Each domain is in turn characterized by multiple sub-domains. We begin with the domains of noise and differentiation. However, the main contribution of our model concerns the domain of adaptability, which refers to variation within the same exact motor representation. In particular, we use the terms learning and (social)fitting to specify the portions of motor variability that depend on our propensity to learn and on our largely constitutive propensity to be influenced by external factors. A particular focus is on motor variability in the context of the sub-domain named co-adaptability. Further groundbreaking challenges arise in the modeling of motor variability. Therefore, in a separate pars construens, we attempt to characterize these challenges, addressing both theoretical and experimental aspects as well as potential clinical implications for neurorehabilitation. All in all, our work suggests that motor variability is neither simply detrimental nor beneficial, and that studying its fluctuations can provide meaningful insights for future research.

1. Introduction

The propensity to recognize one and the same (e.g., that object; that person; that action) in all its variations (from different angles, with different hairstyles, through different motor expressions) is a multifaceted and quintessential human talent. The question of how the brain can support this astonishing ability is a critical challenge for cognitive and behavioral sciences. Although recent advances have contributed to shed light on certain forms of this ability, the neurocognitive and computational architectures that support the recognition of the same, despite variations, are far from being fully explored. The key point is that we cannot advance our understanding of this ability without deconstructing it in more fundamental (sub-)domains. Yet even in areas that seem less complex, such as

the motor one, this propensity remains largely a (charming) enigma. Here we critically review the literature on motor variability and propose a new model that supports the idea that one-dimensional antithetical assumptions (i.e., variability is detrimental vs. variability is beneficial) should be overcome. The aim is not only to provide a conceptual framework that better fits recent experimental findings, but also to contribute to unravel the monolithic construct of motor variability. From the simple opening of a door to Roger Federer's dreamy forehand, repeated actions seem at first glance to be effortless and more or less identical in their execution. However, this is not the case, as variability in the execution of actions from trial to trial is ubiquitous [1]. Regardless of one's efforts and perseverance, it is virtually impossible to reproduce exactly the same action (even for Roger Federer).

In the last decades, some components that confer randomness and uncertainty to motor performance have traditionally been considered detrimental [2,3]. In parallel, a complementary perspective has emphasized the beneficial role of variability in supporting sensorimotor circuits during specific operations and learning [4,5]. Researchers generally assumed that an ideal computational machine should a priori isolate or at least minimize the detrimental part of variability while promoting the beneficial one, given its crucial role in motor skills acquisition. However, this supposedly obvious distinction between detrimental and beneficial facets of motor variability seems difficult to operationalize. In other words, it remains unclear when and how motor variability is a feature that promotes action execution or a defect that hampers it. A major source of confusion is linguistic, as terms such as 'variability', 'variation', 'fluctuations', 'adjustments' or 'noise' are often used inconsistently across research fields. The terminological inconsistency is not simply due to individual lexical habits or preferences but is related to the correct modeling of signal/noise dynamics [6]. Separating signal from noise is a time-honored challenge in the motor control literature, not only from a methodological perspective but also from a theoretical one. Anyone familiar with neuroimaging or electro/magnetoencephalography, for example, knows how difficult denoising data can be. Denoising data not only brings algorithmic challenges with artifact removal, but also theoretical pitfalls [6]. Apart from some sort of absolute, static and unchanging notion of 'noise' or 'signal', the main source of disagreement clearly lies in our specific and task-dependent conceptualization of 'noise' and 'signal'. In short, the denoising of data depends on what we consider 'signal' and what we consider 'noise' (accordingly, it is more an epistemological rather than an ontological problem [6]). This leads us to more radical questions about how information is transmitted at different spatial and temporal levels and how it is hierarchically organized in the brain. At an operational level, this also challenges the classical assumption that any intrinsic or non-evoked (i.e. 'spontaneous') activity plays no functionally relevant role in information processing and can therefore be safely disregarded. Recent oscillatory approaches and combined computational accounts on sensory/perceptual sampling have repeatedly demonstrated how rhythmic fluctuations in the neural machinery structure the highly adaptive, dynamic and context-dependent nature of integrative processing in the brain [7,8]. Taken together, all these elements seem to argue that (some) motor variability should be treated as data and not as a disturbing nuisance or negligible deviation from the (alleged) average. In more conventional language, this means that at least some of the variation should be treated as signal [9].

The model we propose in this work benefits from multiple studies exploring different facets of motor performance variation and decomposes motor variability into specific domains (i.e., noise, differentiation, adaptability) according to the specific epistemological topography of variability. *Noise* refers to the factors - largely intrinsic to the brain-body-environment system - that contribute to motor variability. The domain of *differentiation* reflects our open-ended multiple-choice motor vocabulary and, as will be detailed, is not strictly speaking involved in the architecture of motor variability in our model. The core contribution of our work concerns the domain of *adaptability*. It refers to the portion of motor variability associated with trial-to-trial variation within the same exact motor representation, and notably it takes into account both the individual propensity to learn and the individual propensity to be influenced by
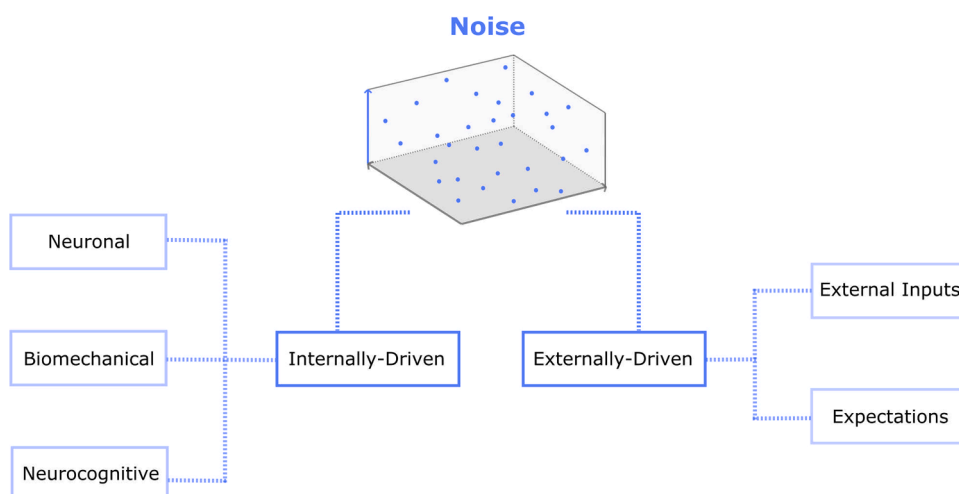
Fig. 1. Schematic representation of the domain of *noise*. The domain of noise is characterized by two sub-domains. The internally-driven subdomain concerns the intrinsic hallmarks that provide randomness and uncertainty to motor performance: (i) neuronal noise, (ii) biomechanical noise, (iii) neurocognitive noise. The externally-driven is in turn composed by external inputs and expectations, which embrace motor variability subsequent to how we process and represent the external world. Single dots within the 3D box represent individual subjects.

external factors. The ambition is not only to promote a more balanced approach to motor variability, but also to reduce controversy arising from inconsistent use of related terms. It is probably not enough to solve the puzzle of motor variability, but it is a promising (and obligatory) starting point.

2. The domain of noise

The first domain of motor variability concerns all stochastic or probabilistic fluctuations in motor output traditionally considered as noise. Pure stochastic noise is unpredictable at any point in time and does not depend on previous values, states or inherent biases of the system (e.g., the probability of each of the six outcomes when rolling a 'fair' die). Probabilistic noise is also unpredictable, but may have some dependence on previous states of the system or biases [10]. As discussed extensively in the literature, several sources of noise contribute to motor variability [3,5,11–13]. These accounts generally focus on the idea that noise is largely inherent in the brain-body-environment system and that we cannot substantially reduce or modulate this source of variability. A primary practical distinction between *'internally-driven' noise* and *'externally-driven' noise* may be appropriate for our purposes (Fig. 1).

2.1. 'Internally-driven' noise

The classical view considers ***'internally-driven' noise*** as an inherent component that conveys an inescapable randomness and uncertainty to motor performance, although it is often negligible and has only a marginal effect on the efficiency of our daily-life activities. Aside from the simplistic assumption that all facets of internal noise are detrimental, there is recent evidence that it can actually be beneficial in information processing. For example, a certain amount of noise in the brain can foster the detection and transmission of weak periodic signals [3,14,15]; it can even help to estimate uncertainty and determine confidence through 'noisy' synaptic processes that impact on probabilistic inference computations [13,16] (for the role of noise correlations and the information-limiting correlations, see [17–20]). In these cases, then, internal noise is a feature (rather than a bug) of brain operations. Brains are dynamic biological systems characterized by both distinct plastic properties and noise at different hierarchical levels (from the molecular to the network level) [21]. Thus, internal variability can result from stochastic/probabilistic biophysical and chemical events that play a role in processes such as spike initiation, propagation or synaptic transmission [5]. For simplicity, we summarize these complex and multi-layered phenomena here as ***neural noise*** [3,21,22].

Undoubtedly, internal noise is also driven by ***biomechanical noise***, which is influenced by factors such as the number of muscles involved in the specific task, their size, or the number of motor units involved [23–25]. This facet of motor variability - that in part overlaps with the composite construct of *execution variability* [26,27]- is closely related to muscle/tendon/joint activity, their structural and organic composition, and noteworthy from the mutual contamination of these body structures. Such a source of variability applies not only to biological systems, but also to robots, where principles such as optimal control and control theory have been applied as potential solutions to problems that correspond to biomechanical noise in humans [28]. While biomechanical noise in humans is due to the complex interaction of muscles, tendons and joints, noise in robots is due to the interaction of the various components — actuators, sensors and other complicated machinery. Each of these components contributes to variability, which makes perfecting robotic movements a constant challenge [29,30]. Ultimately, not only is it virtually unachievable for both humans and robots to completely eliminate interactions between muscles, tendons, or even between actuators and sensors, but it could also compromise efficiency. However, it is worth noting that motor variability, whether due to biomechanical noise in humans or mechanical noise in robots, is not always a sign of error or inefficiency.

Furthermore, we cannot ignore the fact that considerable motor variability in humans is also related to generic and non-specific fluctuations in individual motivation, concentration, and more generally in task-independent fluctuations of neuropsychological functions. We propose to group these aspects under the broad construct of ***neurocognitive noise***. Indeed, there are myriads of task-irrelevant aspects that play a more or less significant role in the way in which we encode, process, reply and ultimately perform our actions. For example, our general (non-specific) attitude toward people impacts the way in which we pass this (specific) glass of water to another person; or even the general (non-specific) architecture of attentional mechanisms (e.g., zooming-in, zooming-out, spatial distribution) impacts the way in which Rafael Nadal organized his (specific) reply to Roger Federer's forehand [31–37]. Thus, even non-specific and task-independent components play a role in trial-by-trial motor variability fluctuations. We will return later on specific and task-dependent components.

2.2. 'Externally-driven' noise

Although some early models assumed that noise depends primarily on perturbations that occur during motor performance, a not-marginal portion of motor variability also derives from processes that occur prior to motor performance [38–40]. Consistent results show that how one processes and represents ***external inputs*** contributes to subsequent motor variability [41]. For most readers, this conclusion may not seem so original. Indeed, the fact that a substantial part of motor variability is determined by intrinsic and extrinsic properties of objects has been widely documented [42,43]. Imagine grasping a piece of apple pie: properties such as temperature, size, weight, but also orientation and position would influence the way we grasp it. What is less trivial is the fact that these properties are far from being naively 'objective' and 'absolute' [44]. Motor variability may indeed depend on how objects are perceived, as shown by [45]. This perspective is consistent with Wagman & Carello's claim [46] that tools expand an organism's perceptual and action capabilities, emphasizing the dynamic relationship between perception, action and the external world. Object features and affordances can therefore be better described as multi-layered and dynamic estimations that depend largely on individual ***expectations*** (or priors)

[47]. Accordingly, both sensory inputs per se and individual estimation of these inputs are factors driving one's (inter)actions [48,49]. For simplicity, we refer to such sources of motor variability as *'externally-driven' noise*. However, we are aware that the term 'external' can be misleading and that it is better to acknowledge the 'internal' source of 'externally-driven' noise as well[1]. Thus, what one hears or sees depends on both 'external' sensory input and 'internal-external' expectations (e.g., memory-driven; statistical perceptual regularities) [50]. In other words: we actively gather sensory information rather than passively register it [51]. In addition, it is worth noting that priors are not set in stone. They reflect the agent's current model of the world, and they are dynamic [52,53]. Sometimes they can even be anomalously dynamic, resulting less adaptive [54–56]. In general, volatility of expectations plays a significant role in adaptation by increasing/decreasing the variability of motor performance depending on the specific scenario. In computational neuroscience, the question of how the brain functions as a predictive processing machine is the subject of a large, lively and stimulating debate [50,57–64]. Taken together, and beyond non-marginal distinctions, these accounts share the idea that perception is an active and constructive process. That is, what one perceives depends largely on a complex set of priors that should support the brain's attempts to predict the incoming sensory input [47]. Clarifying how the brain combines the use of priors to direct perceptual processing towards expected events [65,66], and how it uses these priors to maximize sensitivity to unexpected outcomes [67,68], is a challenge for future research, including that in computational neuropsychiatry [69–71]. A convincing demonstration of the fundamental loop linking priors, sensory input and motor variability is reported in an elegant study investigating the modulation of the safety margin of grip force (GF) [72]. Engineering design classically assumes that the motor system establishes a safety margin above the level of force normally sufficient to complete the specific task in order to reduce the risk of slippage during grasping. Although most models assumed that the safety margin is computed based on the expected dynamics of the load force (LF), Hadjiosif and Smith [72] suggested that this is not the whole story. They demonstrated that the GF control is three times more sensitive to the LF volatility (standard deviation) than to its mean value. In other words, we keep the margin of safety small when volatility is low, while increasing it to prevent a slip when volatility is high. This is to say that if we are holding an object that we think might suddenly move or change its force (high volatility, e.g., a live fish wriggling in our hands), we will grip it tighter than if we are holding a stable object (low volatility, e.g., a book). In fact, in the latter case, we do not need to exert as much extra grip. This is analogous to the wise car driver who keeps a greater distance from erratic vehicles, or the prudent skier who pays more attention to the irregularly descending snowboarders [73].

Although this is inconsistent with the monolithic view of noise, its decomposition (Fig. 1) into more coherent sub-domains does not imply that the brain is noiseless. *Au contraire*, noise is ubiquitous in the brain-body-environment and to some extent constitutive of action. However, it should be clearly distinguished from other domains of motor variability.
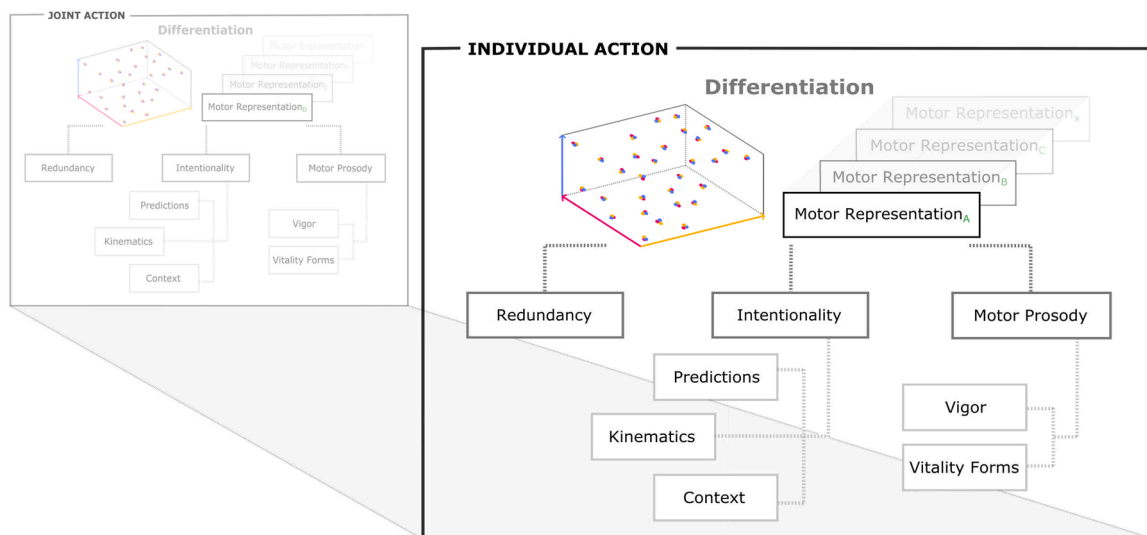
3. The domain of differentiation

We use the term *differentiation* (that in part overlaps with the composite construct of *'strategic variability'* [27] or *'planning variability'* [5]) to refer to the domain that reflects our open-ended, multiple-choice motor vocabulary. Constitutive elements of this domain are i) *redundancy*, defined as the potential motor solutions offered by the degrees of freedom of our musculoskeletal system [74,75], ii) *intentionality,* defined as the specific motor solutions associated with a specific intention [76], and iii) *motor prosody,* defined as the specific motor solutions that are associated to the specific valence of an action [77,78] (Fig. 2).

3.1. Redundancy

The right upper limb of a healthy individual consists of 32 bones connected by about 34 joints. Each of these joints has a different number of degrees of freedom, with a combined total nearing 36. This number far exceeds the 6 degrees of freedom needed to position any of the body segments in a certain position and orientation (e.g., to place the hand correctly on a computer mouse or to hold a smartphone securely without it slipping). Considering that the upper limb houses about 58 muscles, it is easy to imagine the wide range of kinematic configurations and force combinations the body can use to perform a given movement [74,79]. The term *redundancy* captures this sub-domain of motor variability. From the everyday scenario of reaching for a glass with the left or the right hand, holding it by the stem or by the glass itself, to the self-evident observation that a healthy adult of average stature can cover ten meters with twelve, thirteen or even fourteen steps, it is clear that humans exhibit a range of motor variability, in everyday activities. We can choose optimal, suboptimal or sometimes even bizarre solutions (e.g., performing a strange twisting movement to approach a glass), and this naturally leads to motor variability. Imagine traveling from Milan to London to attend Federer's last match of his professional career at the Laver Cup. You are likely to choose the train, the plane, or at most the bus; but the bicycle and the walk are also a priori potential options, even if time constraints and feasibility probably suggest opting for the previous alternatives. Most likely, the optimal solution would be a combination of them (e.g., walk from your home to the bus station; take the bus to reach Milan airport; arrive in London by plane; take both the train and the metro to get to North Greenwich, and finally walk to the O2 Arena). Although quite ridiculous, you could also opt for a kick scooter or even for a horse-drawn cart. Beyond the redundancy sub-domain, differentiation encompasses the multiple facets of motor representation that reflect action goals, their contextual constraints and motoric nuances [80, 81], as will be described in the following sections.

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[1] It is crucial to note that while terms like 'internal' and 'external' are useful and intuitively understood for the purposes of this work, they can pose epistemological challenges, as highlighted by Husserl in "Die Idee Phenomenologie" [244]. Although we employ these terms for simplicity, in line with Occam's razor, we recognize their potential theoretical limitations.

Fig. 2. Schematic representation of the domain of *differentiation*. The domain of differentiation is characterized by the sub-domains of redundancy, intentionality and motor prosody and refers to the variability that originates from different motor representations. Based on numerous studies in both humans and non-human primates, the construct of 'motor representation' can be defined as the neural and computational representation of a specific motor solution (e.g., grasp-to-eat/gently/with the right hand or grasp-to-pour/gently/with the left hand, etc.). Redundancy refers to the potential motor solutions offered by the degrees of freedom of our musculoskeletal system, ii) intentionality indicates the specific motor solutions associated with a specific intention. Different intentions are encoded in subtle kinematic variations and influenced by contextual and predictive components. Finally, iii) motor prosody indicates the specific motor solutions that are associated to the specific valence of an action. The constructs of vigor and vitality forms can be considered as essential components of motor prosody. In the focus, the schematic representation of the domain is framed for a hypothetical individual action, while behind the panel refers to an hypothetical joint action. Within the 3D box, each triplet of dots represents a single subject.

3.2. Intentionality

Over the last decade, a compelling series of studies in both humans and non-human primates have comprehensively investigated how we 'motorically' represent actions at different levels of the motor hierarchy (i.e., motor representation, see [80,81]). This has been studied from the neural [82], computational [83] and clinical [78] perspectives. Motor representations of actions can exhibit high levels of generalization [84,85], abstraction [86,87] and socially oriented tuning [88–90]. In particular, both contextual (e.g., high-level metacognitive components, low-level motor components, low-level perceptual components, low-level sensory components) and predictive components (e.g., statistical regularities, expectations) play a role in grounding the specificity of a particular motor representation. All of these composite and multilayered features are thought to be mediated by complex neural nodes – including, but not limited to, the parieto-frontal ones - that confer remarkable flexibility to motor representation [91–94]. One of the richest products of these lines of research is probably related to the encoding and understanding of intentions. Once the optimal solution for approaching a bottle is established, it is possible to differentiate the action as a function of the specific intention (e.g., reach - [with the intention] to drink - vs. reach - [with the intention] to pour), leading to clearly quantifiable kinematic differences [95,96]. Moreover, thanks to the mirroring properties of the motor representation, intentions can be motorically understood via the elicitation of the corresponding motor representation [92,97]. This is commonly referred to as 'direct', 'motor-based' or 'from the inside' understanding of intentions [81]. Such a process also extends to scenarios of motor interaction [98–100]. Kinematic cues are indeed employed to communicate the intent to cooperate [99] and to communicate the time and location of upcoming actions during joint tasks [100]. Moreover, individuals are able to use such communicative cues to recognize communicative intentions [98]. Therefore, we use the term ***intentionality*** to operationally define this sub-domain of motor variability. The theoretical and clinical significance is underpinned by a growing body of evidence that points to the readability of motor intention in autism spectrum disorder (ASD). These works both uncover the essentially bi-directional nature of social dynamics and the decoding of motor intention into more basic computations [101–103]. Indeed, different intentions are usually encoded in subtle kinematic variations (information encoding), but successful information processing also requires another phase in which the observer appropriately reads out these variations (information readout) [97,104,105]. Notably, this scenario is complicated by the fact that kinematic information, contextual cues and priors are dynamically combined. How such a combination is regulated in (a)typical development and which aspect (kinematics, context, prior) takes precedence over time remains a matter of debate [106–109]. However, there is no doubt that this dynamic combination per se is part of motor variability.

3.3. Motor prosody

Daily-life motor intentions are not 'cold', 'neutral' or 'aseptic'. They involve at least a minimal degree of coloring by **motor prosody**. We refer to the notion of vigor and vitality form to approach this sub-domain. Vigor is an operational construct that provides a quantifiable (motor) proxy for variables such as subjective 'utility', 'value', 'attitude' or more generally 'reward' [110,111]. It essentially reflects the tendency to move with shorter latency and higher velocity towards stimuli that are judged to be more relevant [112]. One view holds that the amount of reward plays the most important role in modulating vigor [113]. However, and largely consistent with the present work, it has been suggested that the difference between predicted and actual reward plays a central role in the regulation of vigor [114]. That is, the invigoration of action is controlled by a complex set of computations that provide a real-time estimate of subjective value, and this estimate is computed by comparing the expected and actual rewards. Vigor is a continuous variable and a ubiquitous feature of movement. We can assume that individuals oscillate between (extremely) positive and (extremely) negative values of vigor, up to the borderline case of the absence of vigor. The question arises whether vigor is an individual trait-like characteristic that can be consistently observed in repeated measurements, and even whether it is coherently expressed by different effectors (e.g., saccades, head-free gaze shifts, reaching and grasping). Recently, partial evidence has been found that vigor is a stable trait-like attribute, but further research is needed on this point [74,115].

It is worth noting that a somehow different view has been proposed for the study of motor prosody; it implies the operationalization of the construct of 'vitality form' originally proposed by Stern [116]. Depending on our mood or affective state, our grasp can take different forms (e.g., gentle or rude), and this underpins social dynamics in development. The notion of vitality form has been operationalized in neuroimaging and motion capture studies [117–119] and would reflect a quantitative proxy for this primordial 'motor contouring' through which we relate to each other [120]. It has been suggested that this motor colouration representation is mediated by the dorso-central part of the insula, and in particular it has been proposed that vitality form processing is endowed with mirror properties [118]. This means that one evokes a similar motor representation both when performing and observing actions, which in turn opens up the possibility of a 'direct'/'motor-based'/'from-the-inside' understanding of the vitality form of others [80, 102]. Human and non-human tract tracing studies seem to converge in showing connections between the dorso-central part of the insula and the core nodes of the parieto-frontal mirror circuit. In an exemplifying 7T diffusion tensor imaging study in monkeys, seed points were located in the ventral premotor cortex near the dorsal part of area F5, in the parietal cortex between areas PFG/AIP, and in the ventro-lateral prefrontal sector between areas 46v and 12r [121].

Motion capture approaches have been used to quantitatively assess the modulation of kinematic parameters in relation to the expression of vitality forms and to investigate possible peculiarities in the expression of vitality forms in ASD [117,119]. It is noteworthy that these peculiarities might in turn play a role in vitality forms recognition difficulties reported in children with ASD [78, 122]. More specifically, being not prone to (motorically) represent and (kinematically) express vitality forms as neurotypical individuals do, then the motor roots of social dynamics may be less informative for ASD individuals. This would trigger potential cascading effects on the tendency of individuals with ASD to be tuned to the surrounding social context [119]. Future research should further clarify the nature of these peculiarities, for example, whether they reflect a different motor code or no code at all, or a generally poorer/less transparent kinematic code, or even a combination of these factors [88,101,102,119,123,124].

3.4. Concluding remarks on differentiation

A few concluding remarks on the differentiation domain deserve special attention. First, although the examples given in this section mostly refer to individual actions (e.g., Roger reaches to pour gently; Mikaela reaches to drink rudely), there is no doubt that individuals also act together (as briefly described above referring to motor interaction). People walk together, play the piano together, paint together [125]. Joint action can be driven by the synchronization of two or more rhythmic behaviors with respect to phase (i.e., entrainment), regardless of whether this synchronization is actively sought, simply encountered, or even eluded [126]. However, non-rhythmic joint actions may also occur. Alternative views aside, the general idea is that when agents act together, they represent not only their own individual task but also a collective goal. Put more simply, we act together when our actions are collectively directed towards a shared outcome [127]. In this view, joint actions should be distinguished from purely parallel actions: the former require a collective goal that can be represented motorically, leading to interpersonal motor coupling effects (joint-shared action); the latter simply refer to individual actions performed in parallel (joint-parallel action) [128,129]. Please note that in what follows we always refer to joint-shared and not to joint-parallel actions. To return to our aims, we emphasize that all the considerations made in the sub-domains of intentionality and motor prosody concerning individual motor representations can in principle also be applied to joint motor representations. This extends and complicates the scenario considerably, since we should also consider, for example, potentially contrasting motor representations in joint actions (e.g., Roger lifts the suitcase gently; Roger and Mikaela lift the suitcase together, Roger gently - Mikaela gently / Roger gently - Mikaela rudely / Roger rudely - Mikaela gently / Roger rudely - Mikaela rudely). For the aims of the present work, the presence of another actor interacting with us is a modulating factor of motor variability. Second, and partly related to the first observation, both individual and joint actions are not neutral with respect to the addressee or co-actor. This means that 'to whom' and 'who' are additional factors that play a role in modulating motor variability [130]. Interestingly, this has been indirectly supported by studies with non-human primates. Indeed, the motor representation of actions is influenced both by the subjective value of the grasped object [131] and by the presence of a non-social vs. social outcome (e.g., box vs. human experimenter) [89,90]. In the next section, we will focus on the functional implications of these effects.

To conclude, distinct characterizations of the differentiation sub-domains suggest that additional components contribute specifically to motor variability (Fig. 2).

4. The domain of adaptability

A key point is that in describing the domain of differentiation, we have referred to sub-domains of motor variability (i.e., redundancy, intentionality, motor prosody) that involve eliciting different motor representations each time (e.g., grasp-to-lift/gently/ together with Mikaela/in context X_1-Y_1-Z_1; grasp-to-place/rudely/individually/in context X_2-Y_2-Z_2). Although consistent with classical approaches in the literature [9,11,132], these facets of motor variability could be seen - *strictu sensu* - as an expected (or even obvious) by-product of different motor representations. Thus, according to our model, differentiation should not be considered as a genuine part of the architecture of motor variability. More interestingly for our aims, however, a significant portion of motor variability is also related to variation within the same exact motor representation. We refer to this additional domain as ***adaptability*** (Fig. 3). This construct can be defined in terms of variations in motor outputs that depend on our propensity to learn, and on our largely constitutive propensity to be influenced by external factors. This definition gives rise to two pillars that need to be considered in more detail.

First, any learning process should a priori presuppose an initial de novo learning [12]. Although one can speculate that any supposed de novo learning results from a set of already acquired skills (e.g., when Ringo Starr first used drumsticks to drum, he had certainly already used a twig to beat a log), in terms of the narrative aims of our model, we are inclined to accept at least a minimal sense of de novo learning. While this does not solve the theoretical problem of the practical existence of pure de novo learning, it does support efforts to structure the architecture of the different learning components that lead to motor variability. For example, in February 2022, Italian alpine ski racers Sofia Goggia and Nadia Delago had no experience of the downhill racetrack prepared for the Beijing Winter Olympics. For the purposes of this paper, we can assume that their very first warm-up on the Olympic track was a genuine de novo learning experience (i.e., in terms of the particular type of snow, the moguls, the turns, etc.), even though both Sofia and Nadia already had extensive experience of similar racetracks in many other sites. It is certainly true that they have benefited from a number of motor prerequisites (above all, they are exceptional skiers), but in the sense that we propose for our aims, we emphasize the novelty of that specific track for Sofia and Nadia. In line with this account, it can be argued that we face de novo learning in a variety of daily life activities. When this happens, we increase our motor variability to promote exploration of motor solutions and find the one that better fits the activity [5,12,133–135]. Indeed, when learning new tasks, individuals exploit variability and adapt their movements to find optimal solutions through reinforcement strategies. In particular, higher levels of task-relevant variability have been shown to predict faster learning rates across tasks and individuals [4,136]. Returning to the experiences of Sofia Goggia and Nadia Delago in Beijing, it is conceivable that they explored a wide range of motor solutions during their training sessions on the unfamiliar Olympic track. This exploration reasonably served as the basis for their top performances during the official event.

The second pillar concerns the construct of motor interference and, in particular, its effects on motor variability. It has been hypothesized that our motor system is highly permeable to 'external factors'. Motor interference occurs, for example, when there is a discrepancy between the movement we perform (e.g., a horizontal sinusoidal arm movement) and the movement we observe at the same time (e.g., a vertical sinusoidal arm movement) [[137–139], for clinical implications in ASD see [140]]. Other studies examined the effects of another person's action (or even another person's gaze at the object) on the participant's subsequent motor performance
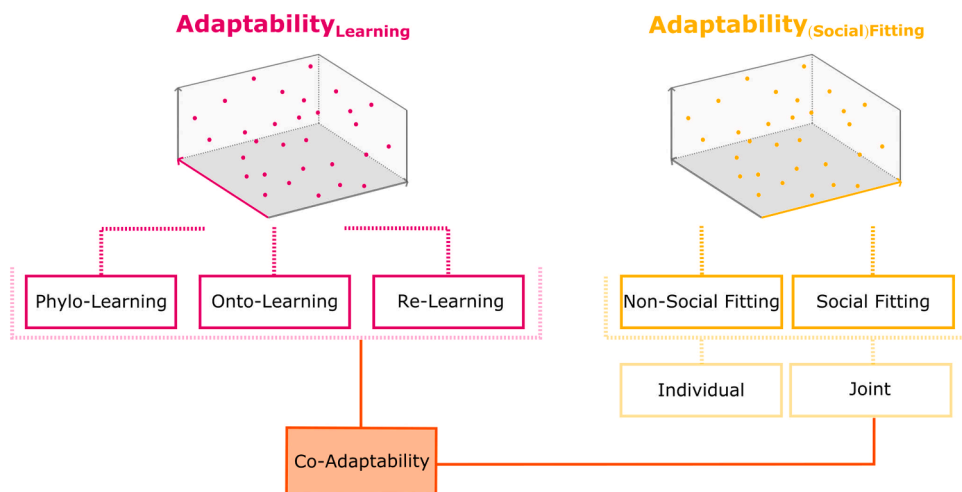
Fig. 3. Schematic representation of the domain of *adaptability*. The domain of adaptability refers to the portion of motor variability that relates to variation within the same exact motor representation. It is characterized by two sub-domains: Learning and (social)fitting. Learning refers to the variations in motor outputs that depend on our propensity to learn. Within this sub-domain there are three different types of learning: phylo-learning, onto-learning and re-learning. The sub-domain of (social)fitting refers instead to our largely constitutive propensity to be influenced by external factors. In this sub-domain motor variability arises from factors that may affect our actions in a situation of non-social or social fitting and in an individual or joint context. Notably, at the intersection between learning and social fitting there is co-adaptability. We hypothesize that co-adaptability is the process that adjusts movement patterns to promote inter-individual tuning. Each dot within the 3D box represents individual subjects.

and found significant modulatory effects on the participant's kinematics [141,142]. Interestingly, a kind of 'transfer of interference' has also been reported in the literature [143], supporting the idea that neurotypical individuals - differently from individuals with ASD [78,140,143] - encode, decode, and then process non-social/social cues, and this operation produces quantifiable motor effects (i.e., motor variability) in their actions [78,144]. All these approaches assume that motor interference does not involve any tendency (implicit or explicit) to adjust individual motor performance to 'external factors' (e.g., other's congruent/incongruent movement, other's action, other's gaze, etc.). Accordingly, the notion of motor interference would not have an overtly finalistic sense, while it would describe the effects of external factors on motor variation in neutral terms. Remarkably for our purposes, both pillars (de novo learning, motor interference) are better represented as *zero-degree of adaptability*, from which we will in turn derive different sub-domains of adaptability. With the term zero-degree of adaptability we refer to the view that de novo learning and motor interference are the basic, level zero, prototypical characterizations of adaptability. To operationalize these prototypical characterizations, we use the terms *learning* and *(social)fitting*. Let us now explore what they mean from a theoretical, experimental and clinical perspective.

4.1. Learning

Probably the most fundamental form of **learning** is that based on the evolutionary perspective (hereafter **phylogenetic learning**). Comparative studies of the evolution of locomotion show that the transition from water to land has represented a fundamental step in the vertebrate lineage [145,146]. The diversity of locomotion modes in animals (e.g., swimming, running, flying and hopping) reflects the evolution of both the motor repertoire and motor networks [147]. How the brain evolved to support new motor behaviors, despite remarkable conservation of expression of key patterning genes, remains a central question in developmental neurobiology. Thus, it has been hypothesized that small changes in the activity of transcription factors may be an important driving force influencing the evolution of neuronal architecture [147]. For example, due to the expression of Hox genes, different motor effectors and locomotion strategies have evolved in the evolutionary lineages of vertebrates, from lampreys to human primates [147,148]. Another example concerns the cerebellum. A recent theory suggests that the cerebellum supports the development of species-specific motor traits useful for survival in different environmental scenarios, and that changes in the expression of the Sonic Hedgehog protein (Shh) are involved in this process [149]. In summary, the multiple modes of action of transcription factors result in inter-species variability at the level of neural circuitry, connectivity and, in turn, neurocognitive and motor abilities [150,151]. This occurs even though aspects reflecting inter-species continuity are permanent [152,153]. Broadly speaking, this demonstrates an evolutionary propensity for adaptation. Returning to our specific aims, this may be referred also to motor variability (which reflects a phylogenetically determined tendency for motor performance to adapt). This would mean that a portion of motor variability may be driven by ancestral and primordial needs guided by evolutionary pressures [154]. To shed light on another facet of motor variability as adaptability, we should encourage a change of perspective that focuses on individual subjects. Motor variability reflecting the tendency (implicit or explicit) to adapt output to promote refined, improved and more skilled specific motor behavior, probably represents our prototypical view of motor learning (hereafter **ontogenetic learning**) [155–157]. This is consistent with the hypothesis that – in both ontogenetic and phylogenetic development - motor variability can promote exploration strategies that facilitate learning (in the sense of optimal solutions to achieve a specific goal) [5,12,133–135,158]. From babies learning to crawl to adults learning a new sport, motor variability leading to exploratory learning appears to be ubiquitous in our development [1,159,160]. Although a remarkable number of studies have examined the complex relationships between movement, motor variability and motor learning, the picture is not entirely clear [4,5, 161–164]. Some studies have focused on adaptation tasks to investigate the role of motor variability as a marker for predicting individual differences in motor learning [4,163,164]. Others have focused on skill learning [12,133] and, in particular, precision tasks that require learning a consistent outcome across trials [157,165,166]. These differences may help to explain, at least in part, the mixed results in the literature. It seems that there is no single (simplistic) relationship between variability and learning that can be generalized to all contexts. This does not mean that motor variability that supports exploratory learning is nonsensical. Rather, it means that complex constructs deserve to be unpacked to avoid oversimplified conclusions. Variability as an exploratory tool to produce better motor performance is important in elite athletes, for example. After persistent defeats, professional tennis players may decide to change their long-standing habits (e.g., grip, rotation, serving movements, etc.), which can affect their confidence as well as their performance and success. During the time Tiger Woods focused on reshaping his golf swing, he failed to win a single tournament for two years [1]. Another example comes from songbirds. They are strongly prone to explore their vocalizations to improve their song when they practice alone; in contrast, male birds significantly reduce the variability of their song when they perform for a potential partner, and this has been explained by the effort in gaining the favor of female birds that seem to prefer stereotyped songs [136,167, 168]. More generally, given that the decision to repeat or vary motor performance depends on the ability to predict the future occurrence of a reward (or punishment), it can be argued that some motor variability is modulated as a function of the probability of a reward. Largely in line with the current work's focus on predictive coding, it has also been suggested that changes in motor variability are sensitive to the history (and estimation) of reward [136,169].

Beyond elite athletes, motor variability plays a central role in the **re-learning** of motor skills after clinical conditions in which processing pathways have been spared [170–173]. Any attempt to elucidate the precise contribution of a specific rehabilitation protocol is at odds with the obvious observation of the inherent complexity of compensatory mechanisms, both at the neural and behavioral level [174,175]. Thus, it is per se difficult to determine the exact contribution of rehabilitation approaches based on the idea that motor variability leads to beneficial exploratory re-learning. This is challenging in stroke patients due to their largely unpredictable neuroplasticity [176]. Another illustrative example is transfemoral amputees who report multiple gait asymmetries due to a variety of factors (e.g., pain at the stump-socket interface, limited muscle volume and strength, low confidence in the prosthesis)

[177,178]. The central clinical problem underlying these examples is clearly beyond the aims of this paper, and we therefore limit ourselves to such a brief overview. In contrast, for our objectives, we need to focus on different facets of motor interference, which we operationalize with the construct of (social)fitting.

4.2. (Social)fitting

De novo learning can be intended as zero-degree of adaptability and, to be approached experimentally, must be operationally transformed. Similarly, we propose the construct of motor interference (which is also intended as a zero-degree of adaptability) to be operationally reframed. One might be tempted to argue that – according to most of the literature - motor interference is a simple, elementary and purely passive phenomenon that does not involve any implicit or explicit propensity to adapt [137–143]. The fact that motor interference is also characterized by more subtle properties provides reasons to resist such a temptation. For example, recent evidence suggests that motor interference may also act as a predictive mechanism [179]. Not only this is broadly consistent with the current work's focus on the individual actively gathering sensory information (rather than passively registering it), but it also suggests that motor interference has more sophisticated properties that can be better revealed when we operationally reconfigure such a construct. Remarkably for our aims, the reframing of motor interference should promote the operationalization of its effective impact on motor variability. We propose to do this starting from the idea that in operationalizing motor interference we go beyond its consideration as a zero-degree adaptability and define it as a sub-domain of ***(social)fitting***. Its modulation is task dependent, and the sub-domain is structured with the non-social fitting and the social fitting part (see Fig. 3). Innumerable non-biological factors interfere with our actions. We define ***non-social fitting*** our propensity to address such interferences in an adaptive manner. For example, walking or running activities deal with perturbations due to different morphologies of the terrain (e.g., asphalt; dirt road; gravel road etc.), or even with our expectations around the morphology of the terrain [180]. In general, studies indicate that destabilizing terrains can decrease dynamic stability during walking [181–183]. To proficiently face them, our brain must flexibly and rapidly modify (i.e., *adapt*) its control strategies. This results in adaptive motor variability [184]. Thus, motor variability resulting from the effort to tackle the peculiarities of the environment (e.g., potential frozen sidewalk if one is walking in Iceland) is a non-social facet of our neuro-biologically driven propensity to rearrange interference towards adaptation.

Walking is not only about adapting to (un)even terrains or obstacles. Very often we should also take into account the presence of other walkers. More generally, we should take into account the presence of other biological actors, as also suggested by convergent evidence for common encoding mechanisms representing the location of self and others in the rat [185], the bat [186] and the human brain [187]. Compared to non-social fitting, this sub-domain clearly differs in the fact that also other actors have at least a (very) minimal degree of propensity to move, react and possibly adapt. We should consider biological actors both in their phylogenetic (invertebrates; vertebrates; mammals; non-human primates; etc.) and ontogenetic development (infants; young children; young adults; professional runners; adults; elderly; etc.). Apart from obvious differences (e.g., degree of self-awareness or dexterity), we have grouped all biological actors under the label of ***social fitting*** to operationalize this sub-domain [188–191]. An intuitive illustration of this sub-domain comes from research that focuses on spontaneous organization of collective behavior. In group-living species such as social arthropods, fish or humans, hundreds or even thousands of individuals can coordinate their behavior without any centralized control system [188]. At first glance, it is a wonderful mystery how such coordination can be achieved. What is clear is that individuals of spontaneous organizations must adapt their behavior to the interfering presence of other individuals, and this can only be achieved through specific modulations of individual motor variability. Additional and converging lines of evidence seem to provide interesting insights into the contributor of motor variability that we have called social fitting [189–191]. For example, pedestrian flows in crowds can be analyzed through the computational perspective of simulation models taking into account crowd density (as a critical variable for crowd safety). Interestingly, social identification with the crowd has been found to mitigate the negative effect of crowd density [190]. It is worth noting that Templeton et al. [191] claimed that 'psychological crowds' (i.e., crowds in which individuals perceive themselves as part of the same group characterized by a shared social identity) walked slower and maintained closer proximity than 'physical crowds' (in which members just share a specific place at the same time) [191]. This could mean that pedestrians take into account a complex and multi-layered set of information to modulate their behavior (their individual behavior as part of a shared behavior), which includes not only low-level elements (e.g., physical constraints such as crowd density) but also high-level elements (e.g., the degree of shared identity). Thus, social fitting sub-domain underlines the peculiar adaptive motor variability (both low level, e.g., crowd density, and high level, e.g., shared identity) resulting from other individuals with convergent/divergent targets.

4.3. Towards co-adaptability

In the previous sections, we have presented the operationalisation of the two pillars intended as zero degree of adaptability (i.e., de novo learning; motor interference) into specific sub-domains (Fig. 3). However, this description could lead to the assumption that learning and social fitting follow clearly separate directions without any convergence. In contrast to this interpretation, recent works consistently describe a phenomenon that leads to motor variability and seems to combine the sub-domains of learning and social fitting. We refer to this seminal sub-domain as ***co-adaptability***. This phenomenon suggests that there is a tendency to adapt movement patterns to promote inter-individual tuning [179,192,193]. First, motor interference not only shows an anticipatory tendency to adapt to another's motor goal (see "predictive motor interference"), but it also shows some degree of tuning with the movement patterns of the co-actor in question. Rocca and Cavallo [179] have indeed shown that our motor behavior during dyadic interactions is influenced not only by the nature of the partner's upcoming action, but also by the specific kinematic profile that the partner uses to perform that action. This would mean that Roger is not only interfered by Mikaela's reaching for a bottle to drink (i.e. Mikaela's motor intention),

but also takes into account the specific motor way in which that action goal is achieved (i.e. Mikaela's particular kinematic pattern). Second, the interindividual similarity of kinematic patterns in the performance of grasping and placing actions in everyday life has been shown to correlate positively with the accuracy of intention recognition [193]. This would suggest that interindividual movement similarity exerts a facilitatory effect in intention recognition, providing additional insight to views emphasizing the role of motor resonance mechanisms in intention understanding [81,95,194,195]. Finally, a very recent approach to interpersonal coordination shifts the focus to the microscopic structure of movements [26,196]. Indeed, Tomassini et al. [192] have shed light on the microscopic structure of interpersonal rhythmic coordination. Their results emphasize that movement intermittency synchronizes between interacting partners and offer insights into the foundational aspects of visuomotor processing that are essential for interpersonal movement coordination. This groundbreaking work opens up the possibility that interpersonal coordination can occur not only at the macro level (e.g., people dancing) but also at the microscopic level of submovements. More specifically, submovements have been found to be actively coordinated in counter-phase by interacting partners [192]. This would imply that motor variability is driven by the propensity to co-adapt one's own action to that of another, even at a very basic (microscopic) level.

Taken together, these studies suggest that largely implicit co-adaptive dynamics, due to both interference and learning, contribute to motor variability. Future research should address both the consistency and implications of this co-adaptability hypothesis in experimental settings. For example, co-adaptability is a priori supposed to be mutual, but if – and eventually how - such a bidirectional dynamic is stable/intermittent, balanced/unbalanced should be further explored. Undoubtedly, this represents a promising theoretical advance for studies concerned with joint actions, because it forces us to consider the possibility that microscopic, dynamic, flexible and co-adaptive motor variability contributes to interpersonal coordination.

5. Pars construens: theoretical, experimental, and clinical challenges

Our model proposes a comprehensive analysis of the distinct domains that contribute to motor variability (Fig. 4). Certain points, however, deserve additional consideration for their theoretical, experimental, and clinical implications.

Whether – and possibly how - motor variability can be a marker of inefficient motor functioning or of specific clinical conditions is
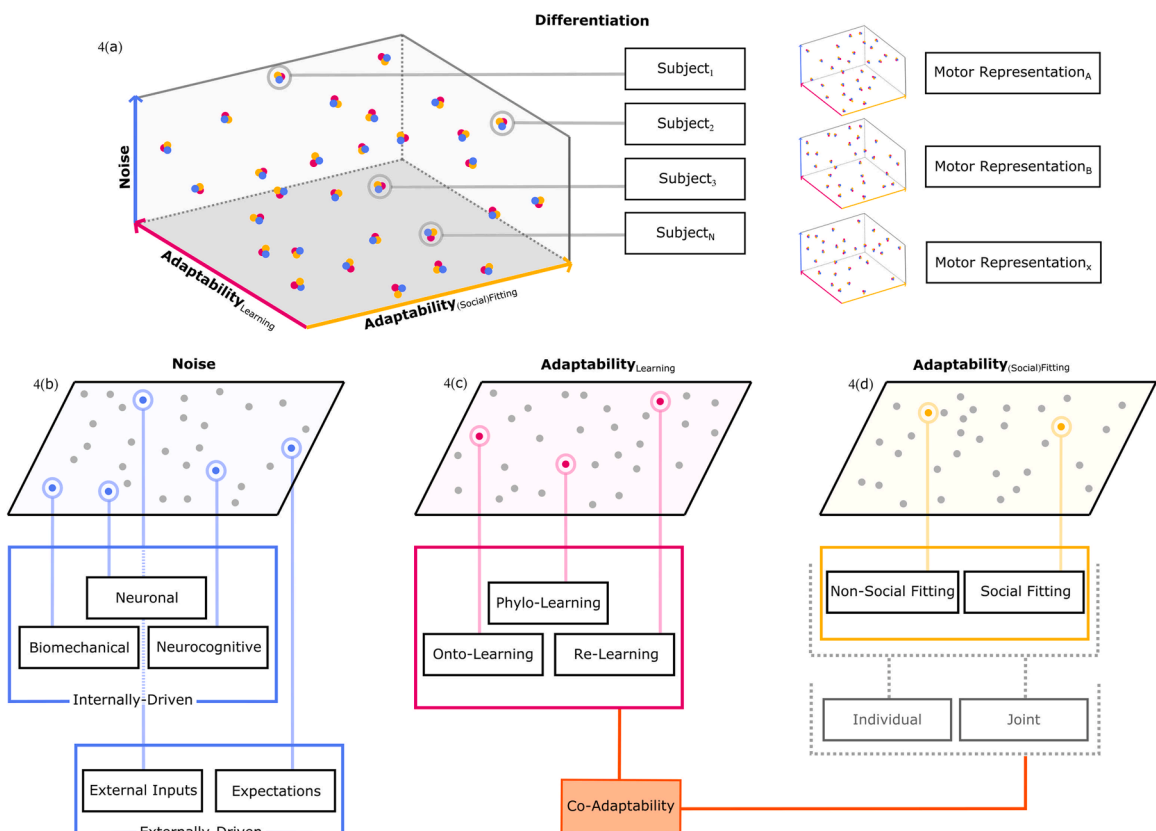
Fig. 4. Schematic representation of the three domains of motor variability. Within a specific motor representation (4a), each individual's motor output is influenced by internally and externally driven noise (4b), as well as by the individual's propensity to learn (4c) and to be influenced by external factors (4d). At the intersection between learning (4c) and social fitting (4d) the sub-domain of co-adaptability emerges. We hypothesize that such a co-adaptive, putatively bi-directional mechanism represents a core factor that regulates motor interactions. Through co-adaptability the motor distance between individuals would reduce, promoting the possibility of an effective interaction.

far from fully understood. The assumption that the distinction between chaotic, random and periodic motor variability accurately reflects beneficial or detrimental forms of variability is intuitive but overly simplistic [197]. This is not to say that increased/decreased motor variability or idiosyncratic fluctuations in motor variability are clinically irrelevant, and the existence of several studies focusing on these aspects may confirm this [11,172,198]. Such relevance is also generally consistent with studies that focus on the variability of different physiological signals [199–201] and with studies that aim to explore the reciprocal influence of motor outputs with other systems [202–204]. Recent work, for example, has combined the analysis of natural locomotion in real-world environments with the individual's gaze behavior [205–207]. To maximize the navigation in complex environments a good degree of motor proficiency is often not enough, then we must direct our gaze to acquire additional (and hopefully relevant) information. In short, walking in a complex environment is not just a matter of our legs. Walking in complex environments requires a flexible combination of gait cycle biomechanics and eye movements in a way that supports competent navigation, for example, in rough terrain [206]. Thus, the way we explore the environment with our eyes essentially determines where we step [207], what destination we reach [208], and also supports the understanding of others' actions [209]. That gaze behavior also depends largely on our prior assumptions, knowledge and expectations should not surprise the reader at this point [50,57–64,210]. Beyond the illustrative case of gaze, comparative analysis of motor and neural variability yields intriguing insights. Several authors agree that brain signal variability is likely to be underestimated in both research [211–214] and clinical settings [21,215–217], although it could provide a useful index of the adaptability and effectiveness of neural systems. Analogous to motor variability, studies with songbirds [167,218,219] and primates [220] have hypothesized that variability in brain signals is important for motor learning. In more general terms, the emphasis on the functional role of brain variability is also largely in line with one of the key premises of the present work (i.e., motor variability is neither simply detrimental nor beneficial).

Over the past decade, the existence of potential links between motor and neural variability has been explored from different perspectives. In a combined non-humans and humans study, it was proposed that both neural and motor variability are characterized by two statistical components: the slow drift of mean responses and the rapid trial-by-trial fluctuations around the drifting mean. Multi-level analyses led to the hypothesis that there is little correlation between the rapid fluctuations of neuronal activity in the dorsal premotor cortex (PMd) / primary motor cortex (M1) and behavior (i.e., trial-by-trial motor variability in reaching movements). In contrast, the magnitude of PMd/M1 neural drifts was found to correlate with the magnitude of behavioral drift (i.e. the magnitude of motor variability across sessions) [221]. On the one hand, this would suggest that PMd and M1 neuronal activity is not responsible for trial-by-trial fluctuations in reaching movements (which account for most of the overall behavioral variability), that in turn may arise elsewhere. On the other hand, Chaisanguanthum and colleagues [221] have proposed as a tentative explanation that the neural/behavioral drift can be explained by an underlying model of error-correcting learning that reflects a continuous process of adjusting the state of the system to reduce performance errors [222,223]. An additional specific focus on the link between motor and neural variability was provided by a very elegant study combining motion capture and fMRI in humans [224]. At the behavioral level, individual subjects showed different magnitudes of motor variability (in terms of movement extent, peak velocity, direction of movement) that were consistent – within individuals – across different reaching movements (4 peripheral targets) and effectors (right or left arm). Subjects who were less variable in their extent of movement to one target tended to be less variable in their extent of movement to all other targets [224]. Similarly, at the neural level, the magnitude of variability in individual brain responses recorded with fMRI in parietal and premotor areas was found to be consistent across targets and arms (e.g., right PMd variability in left arm movements correlated with left PMd variability during right arm movements). In contrast, M1 responses variability magnitudes were not consistent across arms. This seems to suggest that cortical variability magnitudes in parietal and premotor areas are relatively stable individual characteristics, whereas M1 variability magnitudes may represent aspects more related to the type of task or effector [224, see also 225,226]. Noteworthy for the aims of the present work, Haar and colleagues [224] also uncovered a specific relationship between brain and motor variability. Individuals with greater intertrial fMRI variability in the inferior parietal lobule (IPL) showed greater intertrial movement extent variability (brain variability in the right and left IPL explained 24 % of the differences in movement extent variability between subjects). Interestingly, the magnitudes of brain variability in M1 explained only 5 % of the differences in the magnitude of movement variability between subjects. These results seem to indicate that a considerable portion of the variability in movement extent is related to high and complex motor levels (e.g., motor planning, motor representation) rather than to pure motor execution. Taken together, these results not only suggest that the magnitudes of parietal/premotor variability and kinematic variability are relatively stable individual characteristics across different targets/effectors, but also highlight the specific role of IPL (but not M1) in driving the relationship between brain and motor variability [224]. As the authors also point out, there is no doubt that different sources of neural variability could generate motor variability under different experimental conditions [41,72,73,227–229]. Accordingly, one can speculate that motor variability in more complex experimental tasks embodies the sum of multiple convergent/divergent neural sources of variability, indirectly confirming the need to decompose variability into more specific subcomponents. Apart from the considerable theoretical interest, this study also offers potential innovative insights for clinical and rehabilitative applications. Provided that the brain-behavior correlation identified by Haar et al. [224] could be a reliable indicator of a person's functional performance, one could use this subject-specific correlation between neural and motor variability to monitor functional recovery of the arm in clinical conditions characterized by acquired brain damage and spared processing pathways (e.g., stroke or traumatic brain injury). Furthermore, one could imagine adapting similar experimental settings for the lower limbs. So far, these ideas are purely speculative, but they present intriguing challenges and potential future turning points for the complex goals associated with monitoring in motor rehabilitation protocols [177,178,217]. Although – once again – only speculative, motor variability could represent a potential turning point also for rehabilitative approaches based on joint actions. Let us consider this additional hypothetical future scenario.

It is becoming increasingly clear that it is necessary to go beyond averaged subject data, as relevant information can be hidden or

even devalued by relying too heavily on aggregate statistics. One possible hypothesis is that motor variability is a key factor in such a need. The simple point is that the mean group effect treats motor variability that cannot be clearly attributed to experimental manipulations as negligeable nuisance or measurement error. However, this assumption is clearly too simplistic [21]. Although aggregate statistics have been an undeniable tool for promoting scientific progress in recent decades, there is a danger that they are not sufficient [230]. One of the more compelling arguments is based on the fact that the brain of a person who attributes a specific intention to another's action via the motor pathway [80,95,96] does not respond to a supposedly 'ideal' kinematic average measure. Attribution of intention in the real world requires a real-time estimate of the intention information encoded in the specific action, and this can only be achieved with kinematic measures from a single trial [97,101]. This shift in perspective on single-trial resolution was originally inspired by mathematical advances in describing how sensory information encoded in a neuronal population is read out to make behavioral decisions in a single trial [105,231], and more generally by the advantages that can be attributed to the analysis of single-trial population analysis over traditional single-cell studies of trial-averaged responses. Indeed, in the presence of ambiguous information at the single-cell level, the population neuron level can provide more clearly interpretable information [232] (for the seemingly paradoxical effects of trial-to-trial neural covariations on the encoding and readout of sensory information, see [233]). Remarkably, such a scenario fits well with approaches that assume the existence of an *individual motor fingerprint* in upper limb movement patterns and in walking [74,124]. These approaches basically assume that each individual has a specific (and unique) motor signature that is recognizable in her/his actions. One hypothesis is that motor variability may play a role in underpinning an individual's motor fingerprint (in terms of upper limb actions, walking, etc.). In other words, motor variability would contribute to the individual motor signature as if it were a space for the expression of individual motor characteristics during movement. Supposing that motor variability encompasses critical properties that characterize individual motor fingerprints, then we could force further our conjectures. Thus, an additional hypothesis is that motor variability may contribute to provide the space for the (kinematic) reduction of motor distance between co-actors during joint actions (basically indicating an operationalization of the co-adaptability sub-domain) [179,192,193]. Whether and how such an approach overcomes its purely speculative status and rises to the rank of experimental evidence needs to be clarified by future research. Should the status of scientific evidence be achieved, it will be interesting to also investigate possible rehabilitative effects on motor social dynamics (i.e., on the tendency to adapt to the motor patterns of others). The precondition for all these conjectures is, of course, the identification of reliable quantitative indices of individual motor fingerprints, which, in turn, should allow us to calculate the motor distance between co-agents [234–236]. We believe that this and related challenges will take a central role in the context of motor neuroscience in the coming years.

6. Conclusion

The source and functional significance of motor variability have attracted much attention in recent years. Here we proposed several ramifications to model the contribution of motor variability to the propensity of individuals to act and adapt in a dynamically changing environment. The preliminary goal was to create a precise lexicon that goes beyond the generic and monolithic use of the term motor variability, which has severely limited efforts to clarify both its sources and its functional meanings (plural) in recent decades. In particular, we have attempted to propose new terminological choices guided by the rigorous and thoroughly characterized (sub-)domains of motor variability. In brain sciences, the need to decompose constructs that combine different levels of description, variable internal robustness or coherence, and multifaceted operational meanings has recently been addressed for – among others – constructs such as 'motor imitation' [195], 'theory of mind' or 'mindreading' [237,238], 'social brain' [239], 'biological movement' [240], and 'causality' [241]. Here we acknowledged these and similar efforts and ideally wanted to replicate their stance for the construct of motor variability. We began with motor variability in the context of the domain we referred to as *noise*, and then we described that related to the *differentiation* domain (that finally was kept out of our model of motor variability). However, the main contribution of the present work likely concerns motor variability related to the domain of *adaptability*. This specific domain is concerned with that part of motor variability associated with trial-to-trial variation within the same exact motor representation [75]. Motor variability as adaptability concerns, on the one hand, the portion of motor variability associated with our propensity to learn and, on the other hand, the portion associated with our largely constitutive propensity to be influenced by external factors. We have used the sub-domains of learning and (social)fitting for referring to these portions of variability, respectively. A particular focus was placed on motor variability related to the specific sub-domain called co-adaptability. It not only reflects the convergence of the two basic pillars (i.e., de novo learning and motor interference) that we have described in detail in the current work. It also brings innovative and fascinating theoretical, experimental and clinical challenges for the future of motor neuroscience. Most importantly, it opens up fascinating challenges for the convergence of motor neuroscience and neurorehabilitation, even if these are largely speculative at the moment.

The aim of our work was to build a lexicon of motor variability and unravel the complex dynamics of the different computations that contribute to motor variability. One important aspect that emerged from the analysis of the different factors contributing to motor variability is the presence of predictive mechanisms that strongly influence the modulation of motor variability itself. Even though the brain has remarkable information processing power, the computational demands of a dynamically changing environment necessarily require the use of predictive accounts to facilitate the processing of myriads of simultaneous information [210]. Neglecting the influence of predictive coding on fluctuations in motor variability would therefore lead to a huge misunderstanding [13]. This is also broadly consistent with the claim that in many tasks, especially complex ones, suboptimal inference is a dominant component of behavioral variability [73]. Although the focus on this aspect is relatively rare in motor neuroscience [41,242,243], it does not seem to be as innovative outside this field. For example, it is well known that the main factor limiting the performance of image recognition software that uses artificial intelligence is not the amount of internal noise of the camera. Humans perform more accurately, even though most digital cameras have better optics than our eyes and more pixels than we have cones [73]. The main factor contributing to

superior human performance is the quality of the algorithmic architecture that performs the inference, which in turn is primarily influenced by the approximations used. In short, just as walking in a complex environment is not just a matter of our legs, recognizing Roger Federer in a picture is not just a matter of our eyes.

To conclude, the factors that contribute to motor variability are considered separately in our model, but they undoubtedly interact with each other. The resulting motor variability should therefore probably be considered as a by-product of such a dynamic and largely unspecified interaction. Deconstructing multiple convergent/divergent factors contributing to motor variability supports a deeper understanding of their functional role in both non-clinical and clinical populations and provides intriguing insights for future theoretical, translational and rehabilitative turning points in behavioral and brain sciences.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

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