Review

Motor invariants in action execution and perception

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Abstract

The nervous system is sensitive to statistical regularities of the external world and forms internal models of these regularities to predict environmental dynamics. Given the inherently social nature of human behavior, being capable of building reliable predictive models of others' actions may be essential for successful interaction. While social prediction might seem to be a daunting task, the study of human motor control has accumulated ample evidence that our movements follow a series of kinematic invariants, which can be used by observers to reduce their uncertainty during social exchanges. Here, we provide an overview of the most salient regularities that shape biological motion, examine the role of these invariants in recognizing others' actions, and speculate that anchoring socially-relevant perceptual decisions to such kinematic invariants provides a key computational advantage for inferring conspecifics' goals and intentions.
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0. Introduction

Imagine having a meal with a friend. You are enjoying each other's company when your friend suddenly moves his/her hand to reach for something on the table. While this happens, you immediately start to gather information about what is going on and look at the shape of the hand as it proceeds toward its goal; for example, you may rule out whether your friend wants to grasp a spoon or a bottle. This information might be so compelling that if the object is too far from him or her for comfortable reach, you may even choose to pass it on to your friend before the action is

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over. Without even noticing, you have just taken advantage of one of the kinematic invariants that shape human motor behavior – in the example at hand, the maximum grip aperture – not only to understand what was happening, but also to modulate your own behavior in a socially congruent manner.

A large body of evidence indicates that the motor repertoires of human beings – and animals in general – are characterized by a number of kinematic invariants. However, an overview of all these invariant attributes of motor behaviors in a unifying framework is currently missing. The goal of this review is to assess the state of the art in this vast field of research on motor control and provide a comprehensive and integrated view on the role that these characteristics might play in the perception of others' actions.

The present review comprises three main parts. In the first part, we will briefly outline some of the most salient invariants of biological kinematics. We will discuss how these attributes interdependently shape human motor behaviors, spanning multiple hierarchical levels of complexity.

In the second part, we will examine the existing evidence for the role of the same kinematic invariants not just in executing movements, but also in recognizing others' actions and behavioral goals. We will review a large body of evidence illustrating how we rely on these characteristics to interpret movements performed by our conspecifics as their actions unfold.

Finally, in the third part, we will offer a formal perspective on how the brain could infer and exploit motor invariants during action observation. Our proposal starts from the standpoint that the brain uses internal models to control movements and these are tuned to the kinematic invariants embedded in human motor behaviors. Evidence for the existence of internal models encoding robust environmental invariants – such as gravity – already exists, suggesting that the brain is particularly sensitive to regularities in the external world. Crucially, to the extent that the internal models used by the brain to control movement are also reused during action observation, the perceptual representations that the brain forms of observed movements should be automatically tuned to the same kinematic invariants. Based on such arguments, we will discuss the speculative proposal that the main contribution of the motor system – and of its internal models – to action observation could be to process kinematic invariants, as these are the most salient and stable characteristics of observed movements.

1. Kinematic invariants: regular attributes of biological motor behaviors

Biological motion, i.e. movements "*[. . .] generated by biological agents, such as humans and animals*" (Yovel & O'Toole [367], p. 384), is characterized by kinematic invariant attributes which, to the best of our knowledge, have not been outlined previously in a unifying framework. The present section aims to provide a comprehensive description of such kinematic invariants of biological motion, addressing in particular how they may be overall interdependent. To this end, we will follow an order of growing complexity from the point of view of the sensorimotor planning and control processes. Since the study of human kinematic invariants pertains mostly to actions performed with the upper limb (e.g., reaching movements to either point to or grasp something), unless expressly specified, we will use the term *end-effector* to indicate the hand.

"*In the motor control literature, you can find many references to invariant characteristics of movements that – a moment's reflection will reveal – you can vary any time you want. As your hand or some tool progresses to a chosen target, you can make it go fast, go slow, go straight, curve, stop along the way, or just give up and do something else.*" (Shadmehr & Wise [295], p. 495). Despite these lines may appear at odds with the very title of the current section, they nonetheless highlight some of the main features of motor behaviors: That is, the *redundancy* [232,148] or, according to other perspectives, the *abundance* [203,202], as well as the *equivalence* [201,261] of movements. On the one hand, the equivalence principle consists in the possibility to perform the same action with different end-effectors (e.g., writing with the right and the left hand, by holding the pen between the teeth, etc.; for a classic account see Lashley [201]), by virtue of a higher-order generalization of the motor plans (Wing [355]; for an investigation of the neuroanatomical and functional bases of this phenomenon, see Rijntjes et al. [266]). On the other hand, the redundancy / abundance feature stems directly from the high number of biomechanical degrees of freedom that intrinsically characterizes the skeletomotor system, as was first pointed out in 1967 by the Russian neurophysiologist Nikolai Aleksandrovich Bernstein (Bernstein, 1967, cited in Bongaardt [43]; cf. von Helmholtz, 1867, cited in Gielen [120]). In light of this, the presence of invariants in biological motion – as will be described in the following – might represent a successful strategy shaped by evolution, allowing for a reduction of the computational load inherent to the sensorimotor control processes while still preserving and exploiting its extreme flexibility.
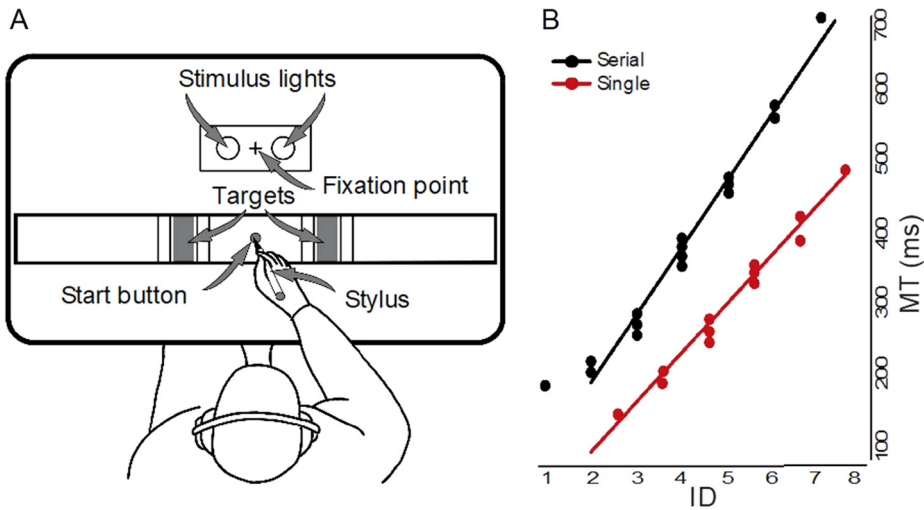
Fig. 1. **Fitts' law provides a mathematical model of the speed-accuracy trade-off. A.** Experimental setup used by Fitts and Peterson [95]. When one of the two stimulus lights came on, participants were required to hit the corresponding target as fast as possible with the stylus. (Adapted from Fitts & Peterson [95].) **B.** Relation between the *index of difficulty* (**ID**) and *movement time* (**MT**). Increasing IDs were obtained by either decreasing targets width or increasing movement amplitudes. Single movements (*red*) consisted in one repetition of an aiming movement from the start button to one of the targets [95]. Serial movements (*black*) consisted in continuous repetitions of aiming movements between targets, without replacing the stylus over the start button [94]. (Adapted from Fitts & Peterson [95].)

1.1. Speed-accuracy trade-off and Fitts' law

In 1899, the psychologist Robert Sessions Woodworth published his doctoral dissertation under the title "*The Accuracy of Voluntary Movement*", which is currently considered a seminal contribution to the field of sensorimotor control (see Newell & Vaillancourt [238]). Although another work – contemporary to his thesis – reported similar observations (Martin & Müller, 1899, cited in Heitz [142]), Woodworth was in fact the first to thoroughly describe the robust and ubiquitous phenomenon which is now known under the name of *speed-accuracy trade-off*. By observing human participants while they performed aiming movements with the upper limb, he noticed that the velocity of a movement is inversely related to the accuracy required by that same movement (Woodworth [364]; for reviews see Elliot et al. [87,86]; Heitz [142]).

More than half a century later, the psychologist Paul Morris Fitts Jr. mathematically formalized such behavior for both serial [94] and single [95] movements (Fig. 1). *Fitts' law* relies on the principles of information theory (see Nyquist [240]; Hartley [138]) and, in particular, on the 17th of a series of theorems proposed a few years earlier by the engineer and mathematician Claude Elwood Shannon (cf. Shannon [299]). Its original formulation, reported hereafter, describes the linear relation existing between the amplitude of a movement, the size of its target and the duration of the same movement:

$$\boldsymbol{MT = a + b \log_2 \frac{2A}{W}} \tag{1}$$

where $\boldsymbol{MT}$ = *movement time*, $\boldsymbol{A}$ = *movement amplitude*, and $\boldsymbol{W}$ = *target width*. Therefore, Fitts quantified the accuracy required by a movement as the ratio $\frac{A}{W/2}$ between its amplitude and the target radius (assuming a circular shape) and identified in its binary logarithm – which is commonly used in this theoretical framework to express information bits (e.g., see Shannon [299]) – an *index of difficulty*, $\boldsymbol{ID}$, of the movement itself [95].

Although a discussion on what could be the correct mathematical expression of equation (1) continued over the following years (cf. Welford [351], chap. 5; Welford et al. [352]; MacKenzie [207]; for a review see Hoffmann [149]), we will not address the details of this debate as it is beyond the scope of the present review. What seems important to underline here is how the speed-accuracy trade-off, as modeled by Fitts' law, represents an invariant attribute of several motor behaviors, involving not only the upper limb but also many other end-effectors (e.g., the lower limb, the trunk, etc.; see Hoffmann [150]): That is, movement duration depends on the accuracy requirement of the task at hand, a requirement that, in turn, grows linearly as the movement amplitude increases and/or as the target width

decreases (see Fig. 1B). If we consider reaching for an object with the upper limb, the time necessary to complete the movement is systematically affected by the distance that separates the end-effector – either the hand or a tool – from such an object, as well as by the object size. Interestingly, a closer examination of the temporal evolution of reaching movements further reveals that object size modulates the end-effector velocity early after the movement start (i.e. at ~10% of movement duration, according to Ansuini et al. [22]; we will return to the implications of this important finding in section 2.2). On the other hand, decreasing movement duration, i.e. increasing its velocity, but keeping target size and distance unchanged (thus providing with the same accuracy requirement), leads to an increase in the endpoint variability (Schmidt [288]). Given that increasing movement velocity requires the generation of stronger force, the variance measured at the endpoint increases as the force developed by muscles increases. This observation can be interpreted according to a property of biological systems known as the *signal-dependent noise* (Berret et al. [33]; Takeda et al. [312]): Such an expression refers to processes in which the noise standard deviation depends on the signal mean (Shadmehr & Mussa-Ivaldi [297], chap. 4), a phenomenon that will be recalled again in this paper (see section 1.4).

1.2. Straight paths and bell-shaped velocity profiles

Despite the high dimensionality resulting from the richness of degrees of freedom that characterizes the skeleto-motor system (Bernstein, 1967, cited in Bongaardt [43]), in unconstrained circumstances the end-effectors tend to move approximately along a *straight path* (see Shadmehr & Wise [295], chap. 18). In 1981, Morasso was the first to describe such regularity, by observing human participants while they reached for targets placed in different positions by holding a manipulandum that could move along two dimensions (Morasso [229]; see Fig. 2A). Several studies confirmed this finding in humans [302,1,156,101] and reported similar results in both non-human primates [118] and other animals [130,129,309]. Noteworthy, such regularity is the result of learning processes that occur early in life [143] and, once learned, remains robust even after perturbations are introduced to alter sensorimotor planning and control processes. The use of glasses with displacing prisms – a manipulation which has been widely (and still is) employed in experimental psychology (e.g., see Rosenbaum [273], chap. 5) – clearly illustrates this point. When subjects are wearing these devices, their visuomotor control appears at first severely compromised. After a short practice, they nevertheless become acquainted with the artificial visual displacement and begin again to perform smooth movements characterized by straight paths. The same phenomenon but reverted – an after-effect of such manipulation – is observed after the glasses are removed (e.g., see Anguera et al. [18]). Despite some exceptions been described when the hand path is on the vertical plane (cf. Atkeson & Hollerbach [24]; Lacquaniti et al. [196]; Papaxanthis et al. [241]) or when movements are performed near the boundaries of the reachable space (cf. Haggard & Richardson [132]; Desmurget & Prablanc [79]), a straight path of the end-effectors seems to be a robust regularity which is inherent to the sensorimotor planning and control processes (see Fig. 2B) as a result of early learning and optimization mechanisms. Indeed, the motor system manages to restore it as rapidly as possible in the presence of perturbations. But which kinematic variable(s) could be targeted by such optimization?

When moving an unconstrained end-effector from its starting position to a target, its trajectory – i.e. the variation of its path over time – shows a sigmoid profile that, after taking its first derivative (which means computing its tangential velocity), becomes bell-shaped. In other words, the end-effector undergoes a first phase of increasing velocity (positive acceleration), it then reaches the peak velocity (null acceleration), to end its motion with a second phase of decreasing velocity (negative acceleration) (see Fig. 2C). Remarkably, the organization of goal-directed movements in two distinct phases – an initial 'impulse' phase followed by a 'current control' phase – was again first proposed by Woodworth [364] in his influential *two-component model* of limb control (we will return to this in section 1.5; see also Elliot et al. [87,86]). However, photogrammetry-based motion analysis had just been pioneered in the 1880s by the photographer Eadweard Muybridge (for a historical review, see Colyer et al. [65]; see also the invention of chronophotography by the French physiologist Étienne Jules Marey in the same period, cited in Pozzo & Pozzo [259]) and was still far from being widespread at the time of Woodworth (who used a kymograph), which prevented him from performing thorough quantitative observations in support of his insight. After similar observations were made also for saccadic eye movements [61], less than one century later it became clear that the *unimodal bell-shaped velocity profile* is an ubiquitous [229,302,1,156,101,100,124], cross-species (Georgopoulos et al. [118]; Bizzi et al. [39,40]; Hogan [152,153]; Gutfreund et al. [130,129]; Sumbre et al. [309]) invariant of biological motion, which generalizes for a large class of movements (e.g., violin bowing and jaw movements; see Nelson [237]; Gracco & Abbs [126]). Apart
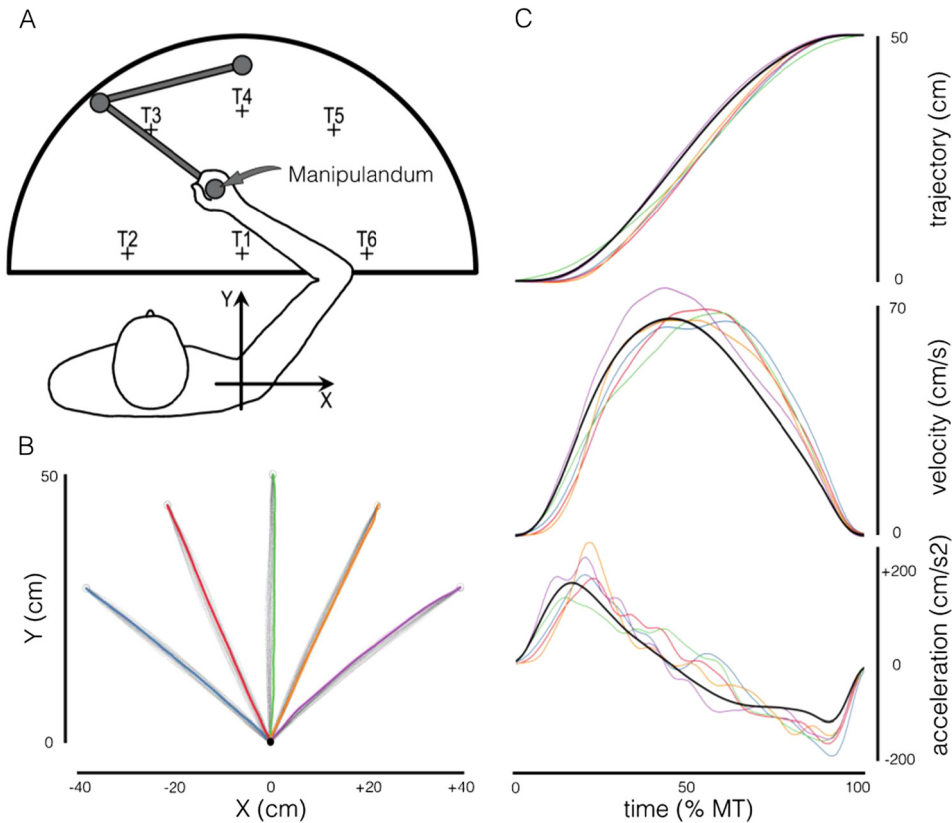
Fig. 2. **Bell-shaped velocity profiles of unconstrained reaching movements. A.** Experimental setup used by Morasso [229]. When one of the six targets (**T1-6**) was switched on, participants performed a simple reaching movement toward the active target by means of a manipulandum. The active target was switched off as soon as it was reached, then another target became active and participants repeated the movement. (Adapted from Morasso [229].) **B.** When reaching movements are unconstrained, end-effectors move along approximately straight paths. In an experimental paradigm similar to the one described in **A**, participants performed repeated reaching movements from a starting position (*black dot*) toward one of five targets (*empty dots*) and back. *Dashed gray lines* show the path of the end-effector in each trial. *Colored lines* show the path of the end-effector in one exemplary trial for each target. (Data from a single participant.) **C.** Kinematic invariants extrapolated from the data showed in **B**, normalized over *movement time* (**MT**). *Upper panel:* Sigmoid trajectory. *Middle panel:* Bell-shaped tangential velocity profile. *Lower panel:* Acceleration. In each panel, the average across all trials (*black line*) is superimposed to the data extracted from the single exemplary trials for each target (*colored lines*) displayed in **B**.

from displaying a typical shape, tangential velocity further scales with the distance covered: Peak velocity increases by increasing the path length [125]. Noteworthy, this characteristic velocity profile remains unchanged despite the different and complex patterns of angles and (angular) velocities of the involved joints [229,302,1,156,101]; further, its optimization in humans occurs in early infancy [346]. Overall, these findings strongly suggest that the bell-shaped velocity profile becomes an invariant attribute of biological motion following a process of optimization aimed at learning to smoothly move any end-effector along a straight path.

1.3. The two-thirds power law and the relation between curvature and velocity

Yet, moving an end-effector along a straight path is not always possible. Indeed, a curved path is sometimes necessary either because of inherent task constraints (e.g., an obstacle that must be avoided to reach for an object) or, more simply, because of the specific goals of the movement at hand (e.g., drawing or handwriting). Although the so-called *isogony principle* – i.e. a piecewise constant ratio between the instantaneous tangential velocity and the curvature radius – was initially proposed after observations collected in drawing tasks [345], it turned out that this principle only holds for some simple trajectories and could not be generalized to all the movements performed along curved paths (cf. Lacquaniti et al. [197]; Flash & Hogan [101]). It was indeed realized that the path usually appears
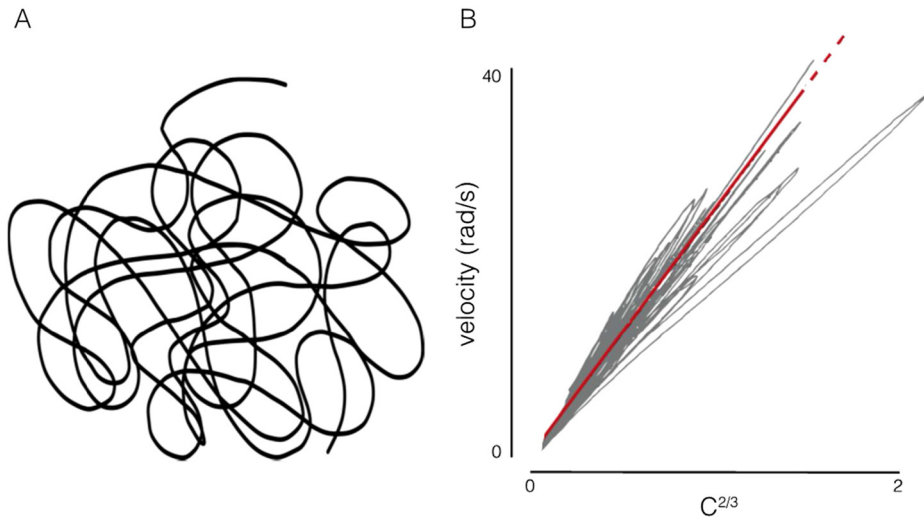
Fig. 3. **The two-thirds power law describes the relation between path curvature and angular velocity. A.** Scribbles provide an example of curved end-effector paths. (Adapted from Lacquaniti et al. [197].) **B.** Diagram illustrating the two-thirds power law. The instantaneous angular velocity of the path showed in **A** is plotted (*gray*) against the path *curvature* (**C**) raised to the power of two-thirds. The average (*red line*) exemplifies the linear relation between the two variables. (Adapted from Lacquaniti et al. [197].)

smooth but not uniform in curvature, the end-effector tangential velocity displays multiple peaks and the local minima between adjacent velocity peaks are approximately temporally aligned to the discontinuities in the path curvature [1,101] – a robust temporal coupling which can already be observed in infancy [346].

In 1983, Lacquaniti, Terzuolo and Viviani successfully modeled the relation between the instantaneous *angular* velocity and the path *curvature* of an end-effector with the following equation, which is now known as the *two-thirds power law*:

$$\omega(t) = k \, C(t)^{\frac{2}{3}} \tag{2}$$

where $\omega(t)$ = *instantaneous angular velocity at time* t, k = *velocity gain factor*, and $C(t)$ = *path curvature at time* t (Lacquaniti et al. [197]; Fig. 3). The value of the velocity gain factor k depends on both the movement total time and the length of the trajectory segment [340], but remains approximately constant throughout the execution of relatively long tracts of the path [197]. Its changes occur either at points of inflections or, in the particular case of drawing movements, at junctions between figural units (e.g., see Viviani & Cenzato [338]). Given that $\omega(t) = \frac{v(t)}{r(t)}$ and $C(t) = \frac{1}{r(t)}$ (where $v(t)$ = *instantaneous tangential velocity at time* t, and $r(t)$ = *radius of the path curvature at time* t), by substituting these quantities in equation (2) and after simplifying, the following relation between the instantaneous *tangential* velocity of an end-effector and the *radius* of the path curvature is obtained [197]:

$$v(t) = k \, r(t)^{\frac{1}{3}} \tag{3}$$

or its equivalent form:

$$v(t) = k \, C(t)^{-\frac{1}{3}} \tag{4}$$

In fact, equation (3) [344,336,176,96,34,205,75,219], along with the equivalent equation (4) [54,8,316], is the one that is most commonly used in the literature, so that some works even refer to it as the *one-third power law* (e.g., see Levit-Binnun et al. [205], and Thoret et al. [316]).

Overall, the two-thirds power law implies a non-linear increasing in the velocity of the end-effector as path curvature decreases (i.e. as the radius increases). By the same token, as the path radius decreases (i.e. as its curvature increases) the end-effector velocity shows a non-linear decreasing, which is in line with the above-mentioned observation [346,1,101] that each local minimum between two peaks in the tangential velocity is roughly temporally aligned with a corresponding local maximum in the path curvature. Although some violations to this model have been reported (e.g., cf. Plamondon & Guerfali [253]), the two-thirds power law appears to be a robust property of upper

limb movements along curved paths (e.g., see Viviani & Schneider [342]). Other studies have shown that the same law applies equally well to movements performed with other end-effectors, such as smooth pursuit eye movements [77], speech movements [313] and movements of both the body center of mass [145] and the foot [162] during gait, further supporting its ubiquity in human motor behavior (see also Zago et al. [374]).

1.4. A rule to smooth them all: the minimum-jerk model

So far, we have outlined two robust kinematic invariants that characterize the trajectories of biological motion: The unimodal bell-shaped velocity profile in movements performed along straight paths, and the two-thirds power law which relates instantaneous tangential velocity and curvature in movements performed along non-straight (i.e. curved) paths. Notably, both these invariant attributes emerge as solutions adopted by the motor system to address a common problem: Performing movements characterized by smooth trajectories beginning from a starting point and ending on a target. In light of this, several works have investigated whether one single kinematic parameter could provide a general explanation for this typical motor behavior within a framework derived from optimal control theory (for a review see Todorov [318]).

In 1982, Hogan analyzed data collected during the performance by human subjects of voluntary movements with their upper limb and identified such kinematic parameter in the movement 'jerk'. Jerk is the third derivative of the displacement or, in other words, the rate of change in the acceleration of the end-effector. According to this perspective, a movement is smoother the more sensorimotor control processes succeed in minimizing the cost function expressed by the following equation:

$$J = \frac{1}{2} \int_{t=0}^{T} j(t)^2 dt \tag{5}$$

where J = *total jerk*, T = *total time*, and $j(t)$ = *jerk at time* t. Movements with a minimized total jerk are known as *optimally-smooth* – or *minimum-jerk* – movements [151]. This finding was further confirmed by other works in humans [237,101], non-human primates (Hogan [153]) as well as other animals [130,309]. This work demonstrated also how the total jerk minimization could accurately model movements performed along curved paths and, therefore, already obeying the above-discussed two-thirds power law (see Flash & Hogan [101]; Viviani & Flash [339]; Todorov & Jordan [319]).

More generally, it has been argued that each of the invariant attributes of biological motion that we have outlined so far – i.e., Fitts' law, bell-shaped velocity profile, two-thirds power law and the minimum-jerk model – could be explained by a unifying *minimum-variance theory* [137]. This theory relies on the assumption that the sensorimotor processes involved in planning and controlling goal-directed voluntary movements aim to minimize the signal-dependent noise (e.g., see Jones et al. [170]; cf. also Wang et al. [348]). Whatever the cost function – if there is (only) one – computed by the sensorimotor system is, we chose here to outline in particular the minimum-jerk model because it is based on a both measurable as well as observable kinematic parameter, which – better than other derivatives of the end-effectors position in space (Flash & Hogan [101]; Richardson & Flash [265]; see also Shadmehr & Wise [295], chap. 18; cf. Berret et al. [32]; Polyakov [255]) – robustly describes an invariant attribute of biological motion. Discussing whether the brain of humans and other animals might have evolved one (or more) pool(s) and/or network(s) of neurons to compute and minimize movement jerk (or other cost functions that have been proposed in literature; for a review see Todorov [317]) is however far beyond the aim of the present review.

1.5. Not so smooth after all: movement is organized into submovements

So far, we have highlighted smoothness as a primary feature of goal-directed movements. Yet, Woodworth [364] again came first to realize that some "little extra movements" often appear towards the end of an aiming movement, i.e. during what he denoted as the phase for 'current control'. Woodworth's intuition was indeed that after the largest initial velocity 'impulse', visual (and, to a less extent, kinesthetic) information afford the possibility for applying finer adjustments, improving accuracy at the (obvious) expense of movement speed. More than half a century later, reflections on the speed-accuracy tradeoff continued to be invariably intersected with a lively interest in feedback-based models of motor control (Crossman & Goodeve [71]; Keele & Posner [181]; Beggs & Howarth [28]; Carlton [51];

Meyer et al. [220]; Elliott et al. [85]). The idea that single aiming movements may actually be composed of multiple, discrete units – so-called submovements – reflecting feedback-based error corrections (see Fig. 4, Top) emerged in these same years and provided the basis for different quantitative accounts of Fitts' law. One earliest account – the 'deterministic iterative-corrections' model – posited an incremental process of error reduction that unfolds through a series of submovements, each taking a fixed time to cover a fixed fraction of the remaining distance, therefore reducing the error from the previous submovement (residual) by a comparable amount (Crossman & Goodeve [71]; Keele [180]). The number of submovements needed to travel a certain distance, and thus the total movement time under the model hypothesis, turns out to increase with the movement ID, as entailed by Fitts' law (see equation (1) in section 1.1). In the forthcoming years, several revisions of this initial model were proposed – for example, the influential 'stochastic optimized-submovement' model by Meyer et al. [220] – to incorporate more realistic assumptions on neuromotor noise and better account for the accumulating observations on variability in submovements duration and spatial accuracy. The impact of visual feedback manipulations on the frequency and properties of submovements also became an object of intense investigation, along with the renewed efforts to provide an accurate estimate of visuomotor delays [377,85,87,52].

Indeed, the idea that movement is organized into submovements is historically deeply intertwined with the notion of an intrinsic lag – or 'psychological refractory period' [314,70,335] – within the visuomotor loop. Largely inspired by engineering models of feedback-based servo control, investigation on human motor behavior in response to serial or continuously changing stimuli (e.g., visual tracking) was proceeding in parallel to the research on aiming movements, and was strongly advocating for a discrete, intermittent nature of motor control [69,335,234,224,226,363]. Visuo-motor tracking became a paradigmatic task to probe for intermittency in movement as its feedback-based and (apparently) continuous nature enabled to unmask intrinsic discontinuities in the sense-and-correct process (see Fig. 4, Bottom). A series of studies both in humans [69,335,234,224,226,222] as well as in non-human primates [224,225] showed that continuous tracking behavior is marked by regular speed pulses – i.e. submovements – generated with periodicity of about 2-3 Hz. Within this theoretical framework, submovements result from intermittent update of the motor control signals on the basis of sensory feedback, which eventually translates into small discontinuities in the velocity profile [363,226,116,285]. The extent to which submovements production is conditioned by the availability of visual feedback and/or susceptible to various types of feedback manipulations (e.g., artificially introduced delays) became soon and still is a matter of debate both in the context of continuous tracking [81,291,311] as well as of discrete, aiming movements [85,103,158].

Whereas current views mostly acknowledge the corrective nature of submovements [291,248,285,311], some alternative accounts posit that submovements are not the result of an (intermittent) feedback-based controller but rather reflect inherent (neuro)functional (e.g., Hogan & Sternad [154]) or biomechanical (e.g., Dounskaia et al. [82]) properties of movement production and organization. One of such proposals considers submovements as a 'dynamic primitive', a basic motor unit, whose flexible assembly (also by combination with other primitives) gives rise to more complex movement trajectories [154]. In particular, when movement is slowed down and/or lengthened beyond a certain limit, it would be unavoidably and automatically split into discrete, possibly overlapped, submovements owning stereotyped bell-shaped velocity profiles [242].

Most recently, important evidence is being accumulated also at the neurophysiological level. Some works have shown consistent neural modulations time-locked to submovements generation [248,272] and highlighted the involvement of motor oscillatory activity whose frequency (2-4 Hz) closely matches submovements periodicity [311,134,166]. Altogether, this suggests that intrinsic oscillatory dynamics in the motor system may map directly into movement intermittency, feeding the ongoing debate on continuous vs. intermittent models of motor control with novel insights.

Despite being relatively subtle ('microscopic') features of movement when compared with other ('macroscopic') invariants (highlighted previously), submovements certainly represent a stable, invariant, property of how movements – especially slower ones (> 400 ms) – are executed. After more than one century from when they were first described [364], the neural and computational mechanisms underlying submovements generation as well as their functional significance yet remain relevant open questions in the current motor neuroscience literature.
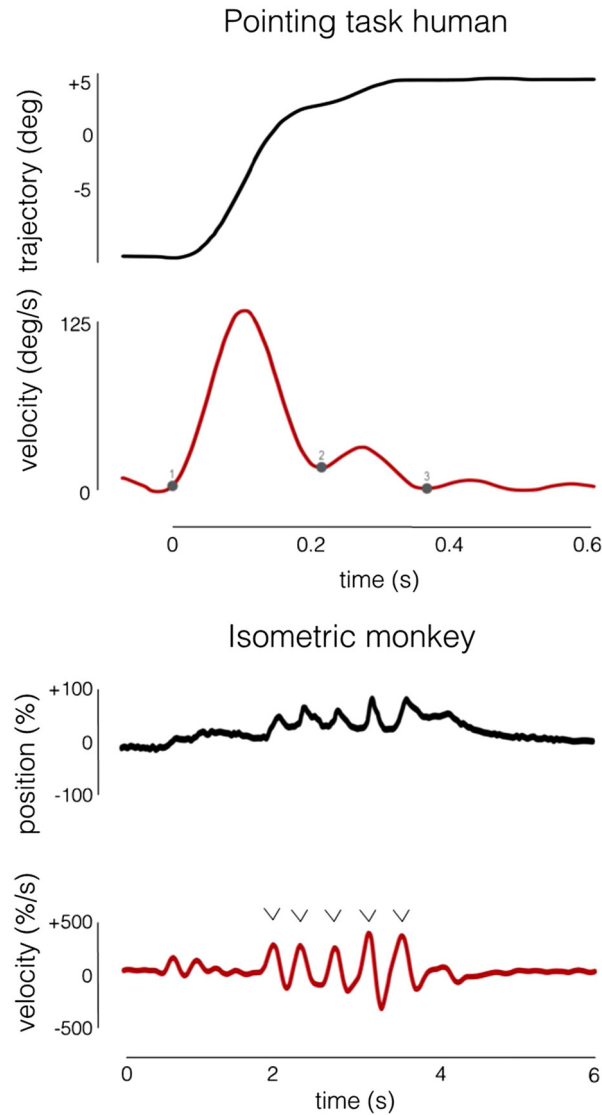
Fig. 4. **Pointing and tracking movements are characterized by submovements. Top.** Example trajectory (*black line, upper panel*) and velocity (*red line, lower panel*) of the upper limb in a pointing task performed by a human subject. The characteristic discontinuities – already observable in the trajectory – are most clearly visible in the velocity profile. *Gray dots and numbers* indicate salient kinematic landmarks: Movement onset *(1)* is followed by the characteristic bell-shaped velocity profile of reaching movements, after which the onset of a corrective submovement *(2)* precedes the overall movement offset *(3)*. (Adapted from Meyer et al. [220]; Original nomenclature: *(1)* movement beginning, *(2)* primary submovement end, *(3)* overall movement end.) **Bottom.** Example of cursor position (*black line, upper panel*) and velocity (*red line, lower panel*) in a visuomotor isometric center-out task performed by a non-human primate. Note the periodic discontinuities highlighted in the velocity plot (*black arrowheads*). (Adapted from Hall et al. [134].)

1.6. The relation between maximum grip aperture and object size

When we reach for an object, it is most often to grasp it. Such reach-to-grasp action implies therefore dedicated processes also for the grasping phase. However, for what pertains the 'macroscopic' characteristics of reaching movements, so far we focused solely on the kinematic invariants characterizing the so-called transportation phase. Even Fitts' law, although factoring in the target size (i.e. the movement goal), considers only the duration of the reaching phase as its dependent variable (see equation (1) in section 1.1). Sensorimotor planning and control processes involved in reach-to-grasp actions should nevertheless take into account the distance of the object as well as its size and shape.
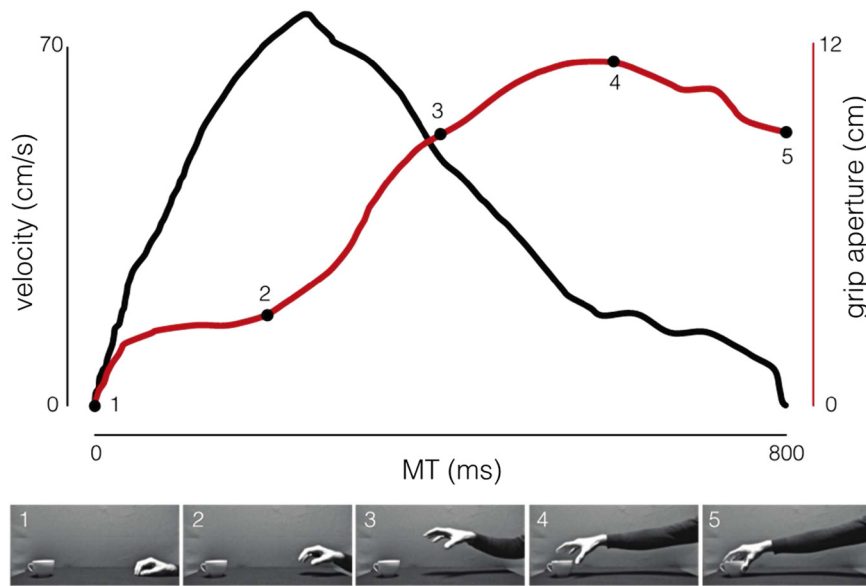
Fig. 5. **Grip aperture is preshaped during a reach-to-grasp movement.** *Upper panel*. Grip aperture (*red line*) is superimposed to the hand tangential velocity profile (*black line*) of a reaching movement, and both variables are represented as a function of *movement time* (**MT**). Note the characteristic biphasic pattern: After a first opening phase in which the aperture gradually increases, the maximum finger aperture is reached (here, at ∼600 ms) and decreases afterward to fit the size of the target object. (Adapted from Jeannerod [164].) *Lower panels*. Photograms of an exemplary everyday reach-to-grasp movement, approximately corresponding to the timestamps displayed above (*black dots and numbers*).

In the early '80s, the French neurophysiologist Marc Jeannerod began to describe goal-directed reach-to-grasp movements in humans and non-human primates. He observed how the grip begins to form during the transportation phase – a process known as hand *preshaping* – and describes a characteristic biphasic pattern: A first opening phase, in which the fingers straighten and the grip opens; And a second closing phase, in which the grip aperture decreases in anticipation to the contact with the object until its amplitude matches the target size (Fig. 5). Remarkably, the end of the opening phase – or, in other words, the time at which the *maximum grip aperture* is reached – occurs consistently after and strongly correlates with the time-to-peak of the hand tangential velocity (Jeannerod [163,164]; Paulignan et al. [245,244]; Becchio et al. [26]; see also Sartori et al. [287], in non-human primates; for different results see Paulignan et al. [246]). Importantly, as already mentioned in section 1.1, the size of the object significantly modulates the grip aperture from the very beginning (∼10%) of the transportation phase [22]. The amplitude of the maximum grip aperture covaries linearly with the object size, i.e. the larger the object the wider the aperture [211,308,165,281,282,88,22], although an interesting modulation related to the ultimate goal of the actions sequence – i.e. grasp-to-eat vs. grasp-to-place identical targets (e.g., see Flindall & Gonzalez [102]) – has been reported as well. Grip aperture is gradually modulated also by the object shape [286], especially whenever undesirable collisions with some of its parts have to be avoided: The higher this risk is, the greater will be the maximum grip aperture (Cuijpers et al. [72]; Verheij et al. [328,327]). Finally, this invariant kinematic attribute appears to hold robustly even when the involved sensorimotor processes are challenged by either low visual resolution (Holmes et al. [157]; Ganel et al. [112,111]; for a different interpretation cf. Utz et al. [324]) or illusory effects (e.g., the Ebbinghaus illusion; see Haffenden et al. [131]; cf. also Smeets & Brenner [301]), suggesting that both the planning and the control mechanisms underlying reach-to-grasp movements are poorly – if at all – affected by ambiguous contextual information (Danckert et al. [74]; for different conclusions cf. Glover & Dixon [122]).

1.7. Intentional effects: end-state comfort and grasp height

When reaching-to-grasp an object, the ultimate movement goal is hardly limited to the actual grasping itself. Indeed, we most often intend to use that object for a future purpose, whereby the grasping action represents only one of a more complex sequence of actions aiming at that same purpose. In such a scenario, the intentionality behind the entire motor sequence may set an important constraint for the selection of the appropriate movements, affecting
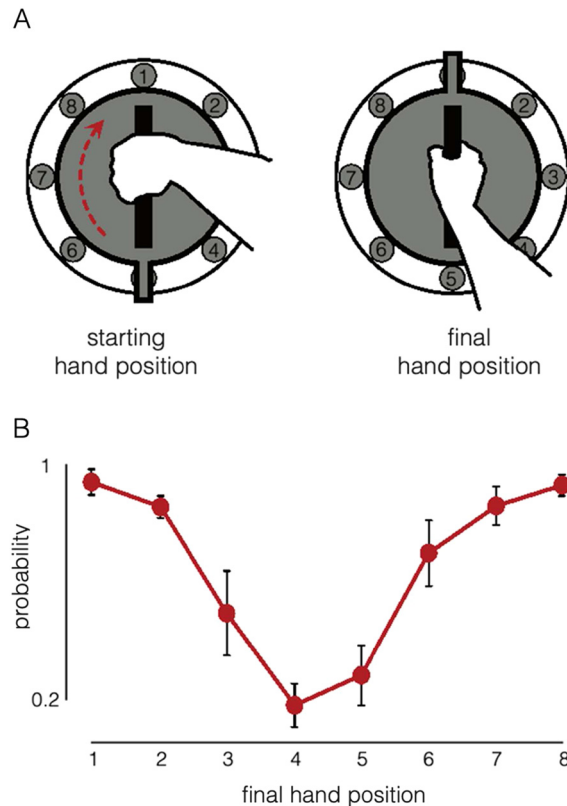
Fig. 6. **The end-state comfort is an example of second-order grasp posture planning. A.** Experimental setup used by Coelho et al. [63]. At the beginning of each trial (*starting hand position, left*), participants grasped a horizontal handle (*black*) fixed over a wheel (*gray*). After a 90° rotation (*dashed red arrow*), they were required to place the left (as in the case shown) or right end of the handle over a target (*final hand position, right*). The numbers indicate both start- and end-points (Adapted from Rosenbaum et al. [277].) **B.** Probability that the final hand position (as numbered above) for the task in **A** affects the choice to place the thumb toward the pointer in the starting hand position. The more extreme would have been the final hand position, the lowest was the probability. (Adapted from Rosenbaum et al. [277].)

the way in which a first-order motor command is planned in favor of a more comfortable, goal-specific second-order posture. Whereas the first accounts of this type of intentional effects were provided for movements different from grasping (e.g., see Marteniuk et al. [212]), they were then thoroughly reported for reach-to-grasp movements by the psychologist David Rosenbaum and his group in a series of works starting in the early '90s. These experiments led to outline the well-known *end-state comfort* (Rosenbaum et al. [278]) and *grasp height* [64] phenomena (for reviews see Rosenbaum et al. [275,274,277]).

The end-state comfort effect consists in performing a grasping movement embedded in a motor sequence by engaging in an effort which is greater than the one required by that same movement when performed in isolation (Fig. 6); Such an extra effort serves the purpose of ending the grasping with a hand posture that is most comfortable for performing the next actions (Rosenbaum et al. [278]). A classic example is the one outlined hereafter: In front of a tray full of inverted glasses, a waiter may decide to grasp one of them with an awkward hand position – e.g., with his thumb pointing downward – with the purpose to lift it up, flip it, and therefore ending with his thumb pointing upward to comfortably fill it with a beverage; That is, he may choose to sacrifice the comfort of his first-order grasp planning by engaging initially in an effortful hand posture to accomplish the actual goal of the entire motor sequence in a comfortable, second-order planned posture of grasping [278,279]. The end-state comfort effect is learned during childhood, and some empirical findings indicate that it is fully developed only around the age of 9-10 years (Adalbjornsson et al. [6]; Weigelt & Schack [350]; Knudsen et al. [185]; Keen et al. [182]; Wunsch et al. [365]; Krajenbrink et al. [192]; for a review, see Wunsch et al. [366]), although other results point toward a far earlier development of simpler second-order grasp planning processes (e.g., see Claxton et al. [62]). Noteworthy, the end-state comfort effect has been widely
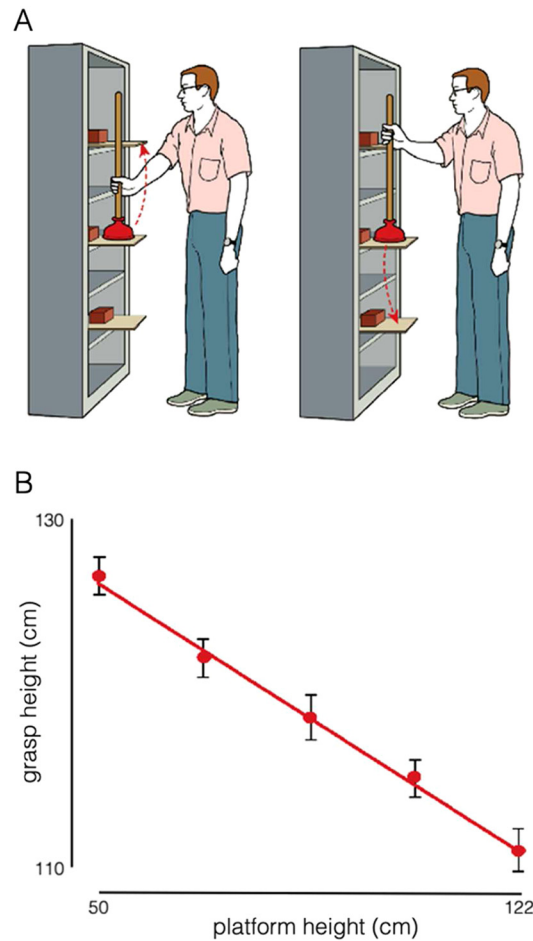
Fig. 7. **The grasp-height effect reflects the height at which we intend to move an object. A.** Experimental setup used by Cohen & Rosenbaum [64]. Participants were asked to move a toilet plunger from a starting shelf to a target shelf (*dashed red arrows*), either higher (*left*) or lower (*right*). (Adapted from Rosenbaum et al. [277].) **B.** Relation between the height of the target shelf and the height at which participants grasped the toilet plunger in the experiment illustrated in **A**. The higher was the shelf to which the plunger had to be moved, the lower participants grasped its handle. (Adapted from Rosenbaum et al. [277].)

documented also in several species of non-human primates [353,59,236,104,376], which suggests how such a capacity may have been selected as advantageous during the evolution of primates in general (see Rosenbaum [273], chap. 2).

The grasp height effect is another example of second-order grasp planning, whereby an object is grasped at different points depending on the purpose intended for that same object, with the aim of preventing ending up the action chain with an extreme posture [64]. A common example is the following: Grasping for a toilet plunger on the floor to move it to a high placement – e.g., a shelf – implies grabbing the plunger lower on his handle; Conversely, when moving the same object from a high placement to a lower one, grabbing its handle higher is advantageous (the choice of this seemingly awkward example is not a random one: see Cohen & Rosenbaum [64]; Rosenbaum et al. [276]; Fig. 7).

The description of the invariant attributes which characterize the kinematics of biological motor behaviors allows us to point out two considerations:

• **Kinematic invariants of biological motion span multiple hierarchical levels of complexity.** Grasping an object implies not only the capacity to produce an optimally smooth, minimum-jerk movement [151,237,101] with velocity scaling according to the accuracy requirements set by the object physical properties (relative position, size) [364,94,95]. It involves also an anticipatory pre-shaping of grip aperture according to the object shape [163,164,245,246,244,286,26] and, more importantly, the ability to incorporate in the ongoing motor plan knowledge about the future intended use of that object [278,279,276,64]. Such a description retraces backwards the top-down

hierarchical organization of the sensorimotor planning and control processes: That is, from an action ultimate goal to the specification of low-level kinematic parameters. Notably, this hierarchical organization modulates all the invariant attributes of the kinematics of a goal-directed movement to match its final purpose, an observation that brings us to the following point.

• **Kinematic invariants of biological motion are interdependent.** Grasping a knife to cut something involves a motor plan that is completely different from the one required by grasping a glass to drink its content. Importantly, such differences are subtler than the most evident one involving the final purpose of each action sequence. Retracing both reach-to-grasp movements starting from their end, emerge different grip postures (i.e. thumb downward vs. thumb sideward), a different maximum grip aperture (smaller vs. larger; Marteniuk et al. [211]; Jeannerod [165]; Roy et al. [281,282]; Eloka & Franz [88]; Ansuini et al. [22]), a different tangential velocity profile (longer deceleration vs. shorter deceleration, independently from the path shape; Hogan [151]; Nelson [237]; Flash & Hogan [101]) and a different requirement in accuracy (higher vs. lower; Fitts & Peterson [95]), which in turn leads to a different movement duration (longer vs. shorter; Woodworth [364]; Fitts [94]). The same observations hold if we consider grasping a knife to either cut something or pass it to somebody. Each reach-to-grasp movement involves a different posture of both the upper limb in general (arm adducted vs. arm abducted) and the hand in particular (thumb leftward vs. thumb rightward, with respect to the knife handle; Rosenbaum et al. [278,279]), as well as – most likely – a different maximum grip aperture (smaller vs. larger, to avoid, for example, accidentally hitting its blade; Cuijpers et al. [72]; Verheij et al. [328]; Verheij & Smeets [327]). Furthermore, it entails a different tangential velocity profile (shorter deceleration vs. longer deceleration), a different accuracy requirement (lower vs. higher) and, therefore, a different movement duration (shorter vs. longer).

These observations show that the sensorimotor system actively modulates the invariant kinematic characteristics of movements for providing solutions – both adaptive and effective – to problems which are intrinsically placed by the processes of sensorimotor planning and control. In such a perspective, their invariant nature should be interpreted in a broader sense, especially when compared to other invariants that characterize the environment (e.g., gravity; we will return to this specific case in section 3.3).

Returning to what reported at the beginning of the present section, not only it is true that human beings can modify their kinematic invariants any time (Shadmehr & Wise [295], chap. 25), but they can also explicitly shape them for delivering meaningful information to observers [330], a phenomenon known as *sensorimotor communication* (Pezzulo et al. [249]; for a perspective article see Vesper & Sevdalis [329]; for a review see Pezzulo et al. [250]). In fact, such a richness of possibilities is provided by the redundancy [232,148] or abundance [203,202] of biomechanical degrees of freedom that intrinsically characterizes the skeletomotor system (Bernstein, 1967, cited in Bongaardt [43]). Furthermore, the phenomenon of motor equivalence results in a higher-order generalization of motor programs, which in turn allows to perform the same action regardless of small local changes that contribute to informational coupling with others (Lashley [201]; Raibert [261]; Wing [355]). A further source of such behavioral variability may be represented by the adoption of individual sensorimotor strategies (e.g., see Berret et al. [31], in reaching behaviors; Cesqui et al. [57,58], in interceptive behaviors; Maselli et al. [213], in throwing behaviors). These *kinematic fingerprints* [284], *dynamic identity signatures* (Hahn et al. [133], in gait) or *perceptual-motor styles* [332] characterize the way in which each different person moves, and may be a possible consequence of how the richness of biomechanical degrees of freedom is influenced by individual variations in anatomical proportions, distribution of masses between the body segments (Bernstein, 1967, cited in Bongaardt [43]; see also Runeson & Frykholm [284]) and even emotional states and/or personality traits (e.g., see the macroscopic gait differences during the triggering to maniac phases in bipolar patients, as described in Kang et al. [177]).

In sum, as we will discuss in the following section, the invariant kinematic attributes provide the observer with an extremely rich set of information.

2. Sensorimotor processes underlie the perception of biological motion

As we have outlined so far, biological motion features several regularities, i.e. invariants. In this section, we ask whether the brain could also use the same invariants during the recognition (as opposed to the execution) of biological motion.

First of all, it is instructive to start from the problem that the brain has to solve when observing – and trying to make sense of – actions executed by another person. It is widely recognized that people can potentially execute movements

with a richness of biomechanical degrees of freedom at their disposal (Bernstein, 1967, cited in Bongaardt [43]). While a lot of research asked whether the availability of several degrees of freedom is a problem or a bless for the person who executes the action (e.g., Latash [202]; see also Rosenbaum [273], chap. 4), here we are more concerned with the fact that it poses a non-negligible problem for anyone who is *observing* him/her in action (for a review see D'Ausilio et al. [73]). The intrinsic redundancy of the motor system is further exacerbated by the inter-individual variation in perceptual-motor styles [332], providing the *observer* of another person's movement with an extremely challenging task [360]. And yet, such a task is performed effortlessly by human beings on a daily basis – how is this possible?

Starting from the early '90s, a seminal series of discoveries carried out in both non-human primates (di Pellegrino et al. [80]; Gallese et al. [109]; Rizzolatti et al. [270]; Umiltà et al. [323]) and humans [91] brought to light the existence of the *mirror-neuron system* (for an opinion article see Rizzolatti et al. [271]; for reviews see Rizzolatti & Luppino [268]; Rizzolatti & Craighero [267]; Rizzolatti & Sinigaglia [269]), which contributes to action encoding through observation. By discharging during both the performance and the observation of either a specific movement ("strictly congruent" cells) or a broad class of movements ("broadly congruent" cells) [109], mirror neurons transform the visual information into an internal motor representation, the outcome of which, importantly, belongs to the observer's motor repertoire [271,267]. Based on these findings, several works have later explored the possibility that action encoding may indeed rely on meaningful, though subtle, kinematic cues.

2.1. Decoding action intentions via intentional effects

Early behavioral works employed *point light display* (**PLD**) manipulations – a technique first introduced in 1973 by the Swedish psychophysicist Gunnar Johansson (Johansson [167]; see also Johansson [168]) – to investigate whether human observers are capable of gathering kinematic information to understand the intentions underlying whole-body movements. To this end, one classic attempt [284] relied on the so-called principle of *kinematic specification of dynamics* (**KSD**), according to which events causal factors are specified by movements ("*[if] dynamic factor **a** influences the kinematic shape of movement **M**, [then] the kinematics of **M** specify **a***"; Runeson & Frykholm [284], pp. 596; see also Runeson & Frykholm [283]). It was shown that human observers are capable of distinguishing the actors' deceptive action goals by viewing only the actors' body representation while they either lifted a heavy box or pretended to do so.

Most recently, a similar PLD paradigm has been used to investigate whether human observers are capable of extracting and decoding meaningful kinematic information to understand whether a reach-to-grasp movement towards a bottle is performed with the goal of either drinking or pouring its content [210]. Humans not only can infer the ultimate purpose of a motor sequence from the observation of its kinematics: They appear to rely on the same kinematic attributes when both minimal (PLD) and full (non-PLD, i.e. natural stimuli) information is provided. In other words, the use of kinematic cues to decode the intention of an observed action may not be limited to (artificial) situations in which no other information is available but could actually play a role also in richer (natural) contexts. Several other studies exploited similar grasp-to-drink vs. grasp-to-pour (and grasp-to-place; Koul et al. [189]) manipulations in more natural (non-PLD) settings [55,191] or different joint-action paradigms [290] to shed further light on action decoding mechanisms (for perspective articles see Becchio et al. [25]; Ansuini et al. [20]; Sciutti et al. [289]; for a review see Ansuini et al. [19]). Altogether, these studies confirm the initial insight for a critical role of kinematic cues in inferring the actors' intentions [290,55], and further show that reliance on kinematic information can be strong enough to override initial context-based expectations [191]. Yet, this capacity may be affected by individual sensori-motor strategies (see Runeson & Frykholm [284]; Hahn et al. [133]; Vidal & Lacquaniti [332]), which may represent a sort of "kinematic threshold" allowing to discriminate between more and less predictable motor behaviors: Indeed, the actor's motor style significantly affects intention decoding by the observer, with some individual kinematic attributes being consistently less predictable compared to others (e.g., see Koul et al. [189]).

The behavioral evidence is supported also by accumulating neurophysiological evidence [304,190,303,243]. In a fMRI study, Koul and colleagues [190] describe the activation of a bilaterally distributed frontoparietal network comprising the *inferior* (**IPL**) and *superior* (**SPL**) *parietal lobules* and the *inferior* (**IFG**) and *middle* (**MFG**) *frontal gyri* while participants observed reach-to-grasp movements to either drink or pour but found no significant difference between the two conditions. Patri and collaborators [243] targeted two of the same network nodes, i.e. the left anterior IPL and the left IFG, by perturbing their activity with *continuous theta burst stimulation* (**cTBS**) during observation

of the same type of (grasp-to-drink vs. grasp-to-pour) actions; they show that the left anterior IPL, but not the left IFG, is causally involved in the observer' capacity to decode action intentions. Compelling evidence that kinematic cues trigger an implicit decoding of the ultimate goal of an observed action sequence comes from a study by Soriano et al. [303]. They exploited single-pulse TMS to probe the *corticobulbar* (**CB**) excitability for a muscle involved in mouth opening and deglutition – i.e. the mylohyoid – on participants observing again grasp-to-drink vs. grasp-to-pour actions and demonstrated anticipatory motor activation only in the former case, i.e. when the future scope of the action (to drink) involves the same muscle recruitment. Such a capacity to distinguish the intentions underlying, at least simple, movements by observing their kinematic features might be learned very early in life, as suggested by infants showing significant *event-related desynchronization* (**ERD**) of the sensorimotor mu rhythm (∼8-10 Hz, considered as a proxy of motor activation; see Hari et al. [135]; Muthukumaraswamy et al. [233]; for a review see Hari & Salmelin [136]) only during observation of actions whose final outcome / goal is non-ambiguous (Southgate et al. [304]; cf. also Geangu et al. [117]). Given that a movement, to activate a motor representation, should belong to the observer's motor repertoire (Rizzolatti et al. [271]; Rizzolatti & Craighero [267]; see also Bonini et al. [44]), this latter finding may be in line with evidence showing a relatively early development of simple second-order grasp planning (e.g., cf. Claxton et al. [62]; see section 1.7).

2.2. Inferring a target object by observing the grip maximum aperture

A number of behavioral studies, employing either perceptual discrimination measures [50,12,21], eye-tracking [11], or a combination of both [280], have investigated whether human observers are capable of using kinematic cues for successfully predicting the object toward which a reach-to-grasp action is aimed to. Earlier works had already pointed out that the observers' gaze proactively shifts toward the forthcoming position of an actor's hand (e.g., see Flanagan & Johansson [98]) and that this anticipatory, task-specific eye shift closely matches the one performed by the actors themselves when they actually reach for, grasp and manipulate an object (e.g., see Land & Furneaux [199]; Land et al. [200]; Johansson et al. [169]; for reviews see Hayhoe & Ballard [141]; Land [198]). More recent works show that human observers can effectively predict both the size and the shape of an object toward which a reach-to-grasp action is performed, be the observed movements either fully visible [280,11,12], partially occluded [21] or even PLD-manipulated [50]. Furthermore, the explicit perceptual judgments [50,12,21] and the implicit oculomotor behavior [11] appear to be highly correlated in time [280]. Notably, as the action gradually unfolds observers rely increasingly more on the kinematic cues related to the grip preshaping and discard potentially ambiguous information – e.g., the actor's gaze orientation toward an object of different size compared to the target object [12]. Such a disentangling process is surprisingly fast, occurring soon after the beginning of the observed movement [280,11,12,50,21], similarly to what was already described for the discrimination of actions goals (see Santello & Soechting [286]; Holmes et al. [157]; Ansuini et al. [22]). This is particularly remarkable considering that the maximum grip aperture during the hand transportation phase is reached approximately when the bell-shaped velocity profile is at its peak [163,164,245, 246,244,26], i.e. roughly halfway with respect to the entire movement duration [229,302,1,156,101], or even later on (cf. Ansuini et al. [22]), suggesting that human beings are capable of using subtle kinematic information as soon as it begins to provide meaningful hints to understand the grasping goal.

The motor system is likely to be directly involved in such predictive processes. Elsner and collaborators [89] delivered *repetitive* (**r**) TMS to either the hand or foot motor areas (M1) during the observation of a PLD reach-to-grasp action toward an occluded object and found that only the former (i.e., effector congruent) significantly delayed the observers predictive gaze shifts. In a following fMRI work, subjects observed a similar reach-to-grasp movement and showed a significant involvement of frontoparietal areas and the dorsal visual stream – with foci located in the *ventral premotor cortex* (**PMv**), the *postcentral sulcus* (**PoCS**) and the *anterior intraparietal sulcus* (**aIPS**) – as long as the to-be-grasped object remained occluded. When the movement was displayed in full view (i.e. with the object completely visible), a strong involvement of the ventral visual stream (for reviews of the ventral and dorsal visual streams see Goodale & Milner [123]; Milner & Goodale [228]) was elicited [315]. As suggested also by the studies reviewed in section 2.1 (cf. Koul et al. [190]; Soriano et al. [303]; Patri et al. [243]), an effector-specific involvement of M1 [89] and a broader recruitment of a frontoparietal network and of the dorsal visual stream [315] to re-enact the observed actions seems to be crucial when the interpretation of others' actions requires paying attention to their body kinematics (e.g., when the objects which represent the movements goals are occluded). The importance of such a re-enactment may nevertheless be context-dependent: When other reliable visuospatial information is available, it

may be complemented by the involvement of the ventral visual stream [123,228] to improve the overall accuracy of action understanding (Thioux & Keysers [315]; for an opinion article see Kilner [183]).

2.3. Discriminating biological from non-biological motion

To the best of our knowledge, no work has specifically investigated whether the minimum-jerk model is used by human observers to discriminate biological from non-biological motion. Nevertheless, several experiments have employed visual stimuli moving along straight or curved paths according to two kinematic invariants – the bell-shaped velocity profile and the two-thirds power law – that can both be inscribed within the minimum-jerk model (see Flash & Hogan [101]; Viviani & Flash [339]; Todorov & Jordan [319]; recall equation (5) in section 1.4). These studies are reviewed in the following:

• **Recognizing a biological stimulus moving along straight and slightly curved paths.** Behavioral works investigated whether human beings may have a dedicated internal model that allows them to discriminate a biologically compatible velocity from non-biological ones (Pozzo et al. [258]; Bouquet et al. [48]; Bisio et al. [38,35,37,36]; Gavazzi et al. [114]; cf. also Hayes et al. [140]). In an early work it was suggested that observers can rely on their motor competences to reconstruct the occluded part of a dot trajectory as long as its velocity is compatible with the kinematics of biological motion [258]. Motion capture techniques further revealed how both healthy people [48,38] and neurological patients – in this particular case, suffering from Alzheimer's disease (Bisio et al. [35]; cf. also Bisio et al. [36]) – show either *motor contagion* (for a review see Blakemore & Frith [42]) or *automatic imitation* (for a review see Heyes [144]) processes triggered by the observation of a biologically compatible kinematics and independent of the specific visual context (e.g., moving dot vs. human model; see Bisio et al. [38]). These processes similarly hold also when the shape of the biologically moving artificial stimulus increases in complexity (e.g., humanoid robot; see Bisio et al. [37]). Interestingly, human observers are both more accurate as well as more precise in estimating the temporal properties (duration) of moving visual stimuli when their velocity matches a biological (bell-shaped) vs. a non-biological (constant) profile [114].

• **When the path curvature is not slight at all.** A number of behavioral works [337,336,343,344,341,76,176, 96,34,205,316] addressed the same hypothesis by means of trajectories occurring along a curved path. Early experiments provided evidence that human beings are perceptually tuned to visual stimuli when their motion along elliptical paths obeys the two-thirds power law [343,341]. Such an attunement to biological stimuli causes strong perceptual – both visual [344] and kinesthetic [336] – illusions. On the one hand, the visual illusion results in the perception of the biological velocity as being uniform and, conversely, of the non-biological (constant) velocity as being strongly non-uniform [344], whereas it is actually the opposite case (Viviani & Terzuolo [345]; Abend et al. [1]; Lacquaniti et al. [197]; recall equations (2), (3) and (4) in section 1.3). Importantly, the involvement of smooth pursuit eye movements in this robust illusion has been ruled out [76], therefore excluding a possible confounding role of concurrent oculomotor commands. On the other hand, the kinesthetic illusion causes a perceptual spatial stretching of motion trajectory along the direction of speed decrease [336]. More recent behavioral works further show how such a tuning to biological kinematics improves visual motion prediction [176,96,34] and is likely rooted in sensorimotor processes (see Levit-Binnun et al. [205]; Thoret et al. [316]).

Neurophysiological evidence further supports the notion that biological motion is encoded within specific / dedicated mechanisms grounded in the motor system [75,54,219,8]. A first fMRI study performed by Dayan and coworkers [75] found significantly stronger activation of a large network of brain areas – including M1 and the *superior temporal sulcus* (**STS**) in the right hemisphere, PMv and IPL in the left hemisphere and the *dorsal premotor cortex* (**PMd**) bilaterally – when viewing a cloud of dots moving according to the two-thirds power law compared to other non-biological types of motion [75]. Casile and colleagues [54] employed the same technique while participants observed a human avatar displayed on a screen, moving either according to the two-thirds power law or not: Differently from the widespread network described in the previous experiment [75], a more focused activation pattern involving only regions in the left frontal lobe with a significant focus within PMd was found, suggesting that processing the information related to a biologically moving human shape might require the activation of a more restricted brain network compared with that recruited by artificial stimuli moving in the same fashion. This hypothesis was corroborated by Agosta and collaborators [8], who employed single-pulse TMS to stimulate the representation of the right hand in the left M1 while subjects observed either a dot (cf. Dayan et al. [75]) or a human avatar (cf. Casile et al. [54])

following a biological (two-thirds power law) or a non-biological (created by manipulating the exponent in equation (4), see section 1.3) motion trajectory. Interestingly, although both the dot and the human avatar biological motion significantly modulated the participants' *corticospinal* (**CS**) excitability, such a modulation was tightly correlated with the stimulus instantaneous velocity only for the human-like stimulus. This might be in line with other neuro-physiological evidence, which suggests that the distinguishing features of biological kinematics may be unnecessary to elicit an automatic motor activation during action observation as indexed by modulation of the CS excitability by means of single-pulse TMS [67]. Finally, in an EEG experiment, Meirovitch and co-workers [219] found a strong and widespread ERD of both alpha – localized in the central electrodes – and beta – involving also prefrontal electrodes – brain rhythmic activity when subjects observed PLD stimuli moving in compliance to the two-thirds power law, with respect to other, non-biological, types of motion (cf. Southgate et al. [304]).

An optimally-smooth, minimum-jerk kinematics (Hogan [151,153]; Nelson [237]; Flash & Hogan [101]; Gut-freund et al. [130]; Sumbre et al. [309]; recall equation (5) in section 1.4) along straight as well as curved paths appears therefore to convey meaningful information that allows human beings to – at least implicitly – recognize it and discriminate it from non-biological ones [337,336,343,344,341,76,176,96,34,205,258,48,38,35,37,114,316]. In sum, people are capable of using these implicit cues to predict the spatial course of visual stimuli moving accord-ing to biological motion [176,96,34,258], make an accurate and precise temporal estimation of their trajectory [114] and also effectively imitate their kinematics [48,38,35,37]. Such capacities may be mediated by the involvement of a widespread frontoparietal network [75,54,219,8] and these kinematic hints are sufficiently strong to even induce perceptual distortions, on both the visual [344,76,205] and the kinesthetic [336,316] domain. Some works appear to suggest that such kinematic information may be meaningful enough to drive the observers' behavior even when other visual cues might be largely more salient, i.e. when both the path of the observed movement and the shape of the end-effector are fully visible (e.g., see Bisio et al. [38]), in line with other results previously reported for both the intentional effects (cf. Manera et al. [210]) and the maximum grip aperture (cf. Ambrosini et al. [11,12]). Neverthe-less, the possibility that kinematic cues are sufficient to override other information – even when it is seemingly more readily available – might be restricted to conditions in which the information density contained in the visual stimuli is limited, as other results also suggest (Flach et al. [96]; cf. Pozzo et al. [257]). It might be that the more we go down levels in the kinematic hierarchy, the more we enter a blurred zone whereby task-independent kinematic invariants of biological motion progressively lose importance to the eyes of human observers, as long as other reliable sources of information can be easily gathered.

Observers are certainly tuned to the invariants that characterize biological motion at a 'macroscopic' level, but are they capable of extracting relevant information also from the 'microscopic' structure of others' movements? In-triguingly, recent findings suggest that submovements can be consistently "read out" also in others' movements and eventually exploited for fine interpersonal movement coordination [321].

2.4. Observing the grip preshaping might not be so strictly necessary after all

In principle, based on the speed-accuracy trade-off (Woodworth [364]; Elliot et al. [87,86]; Heitz [142]) and Fitts' law (Fitts [94]; Fitts & Peterson [95]; Hoffmann [150]; recall equation (1) in section 1.1), an observer should still be capable to infer the size of the to-be-grasped object even when observation of the fingers preshaping is impeded. Indeed, a behavioral work [215] examined eyes movements while participants executed and (separately) observed the same type of movements (based on Fitts' law) and found that fixations, despite being different in number, showed comparable duration in the two conditions. Furthermore, activation of cortical (M1 and *supplementary motor area* – **SMA**) and subcortical (basal ganglia) motor regions during observation of a similar Fitts' task scales with the difficulty – i.e. the ID (see Fitts & Peterson [95]) – of the task [90].

In light of the evidence reviewed so far, we can now draw four considerations:

● **The kinematic invariants of human motor behavior can be proactively shaped by actors.** Especially when involved in a social context, human beings may deliberately choose to vary the invariant attributes of their movements at any time (Shadmehr & Wise [295], chap. 25). To this end, they can exploit the many degrees of freedom afforded by their skeletomotor system (Bernstein, 1967, cited in Bongaardt [43]) to effectively shape the redundancy / abundance [232,203,202,148] and the equivalence (Lashley [201]; Raibert [261]; Wing [355]) intrinsic to their motor behaviors, with the specific purpose of making their actions goal more transparent (see Pezzulo et al. [249]) even in spite of other

available irrelevant or misleading cues (see D'Ausilio et al. [73]). Such a sensorimotor communication (Pezzulo et al. [249,250]; Vesper et al. [330]) strongly depends on the "malleability" of human kinematic invariants, a characteristic that cannot be found in any other environmental invariant attribute (e.g., cf. Sun & Perona [310]; Mamassian & Goutcher [209]; Girshick et al. [121]; Jörges & López-Moliner [173,174]; see section 3.2 and 3.3).

• **The observer's individual motor signature(s) tune(s) action recognition.** Besides the specific intention / strategy of conveying sensorimotor (communicative) signals, every person moves according to his or her own kinematic fingerprints / dynamic identity signatures / perceptual-motor styles [284,133,332], which may be successfully encoded – be the person already known or not – by the observer(s) to recognize who is performing the action (Hill & Pollick. [146]; Troje et al. [322]; Sevdalis & Keller [294]; for a review see Yovel & O'Toole [367]). Furthermore, previous knowledge of the actor's personal sensorimotor style may sometimes even be crucial to correctly interpret the observed action. According to neurophysiological evidence, this may lead to an increasing modulation of the CS excitability during the observation of sensorimotor strategies which remarkably differ from one's own [147].

• **The strong prior knowledge deriving from expertise plays a crucial role in actions encoding.** Whereas the kinematics of everyday movements – e.g., a reach-to-grasp – can deliver meaningful information to any healthy human being (e.g., see Soriano et al. [303], for an eloquent account), the same point does not hold anymore when a less common, highly skilled action – e.g., an athletic gesture – is observed: In this case, the role of expertise – i.e. the repeated exposure to both the performance and the observation of a specific set of motor acts – plays a fundamental role in making predictions of the movement outcome [3,4,300,2,7,334,160,230,331]; Motor training especially seems to be critically involved (e.g., see Casile & Giese [53]; Beets et al. [29]), in line with the importance of the observers' motor repertoire in understanding actions [271,267].

Studies in the field of sport sciences have investigated to which extent expert players are better than either amateurs or novices in extracting, especially under time pressure, information concerning the intention of an opponent by observing his/her movement kinematics (for a review see Müller & Abernethy [230]). For example, experiments with squash [3], tennis [300,160], badminton [2,4] and handball [334] players pointed out how expertise in a specific discipline facilitates the prediction of the direction [3,300,2], the depth [3,4], and the type of stroke [300,160] that is about to be executed by the opponent. Such an improvement (due to expertise) remains intact when visual information is impoverished by using PLD-manipulated stimuli instead of videos [3,4,300,2,230], although the two types of stimuli may prompt different strategies (e.g., cf. Vignais et al. [334]).

Besides conferring finer granularity to the representation of others' actions, motor expertise may also optimize the prediction of future kinematic cues. For instance, Aglioti and colleagues [7] applied single-pulse TMS on the right hand representation in the left M1 of both basketball experts and novice subjects while they observed the execution of free shots (a motor behavior which, in a broad sense, is comparable to a Fitts' task). Results showed that elite basketball athletes can predict the success of the free shots earlier – even before the ball leaves the player's hands – and more accurately than both other experts and novices, and they display a time-specific motor activation during the observation of erroneous throws (see also Vicario et al. [331]). These findings suggest that motor expertise translates into corresponding expertise in encoding others' kinematics by providing with kinematic priors, which are finer-grained and have a longer temporal horizon.

• **Contextual environmental information may be decisive in encoding ambiguous kinematics.** Although informative in many situations, kinematic cues may sometimes be insufficient or ambiguous (e.g., see Flach et al. [96]; Thioux & Keysers [315]). In these cases, contextual information becomes decisive in complementing kinematic information. Parallel to several findings outlining either a complementary (e.g., see Almeida et al. [10]; Kalénine & Buxbaum [175]; cf. also Vankov & Kokinov [326]) or interferent (e.g., see Borghi et al. [45]; Randerath et al. [262]) role of contextual information in sensorimotor planning and control processes (Watson & Buxbaum [349]; for a review see van Elk et al. [325]), recent results point out the importance that such information plays also in understanding others' actions (see Anelli et al. [17]; Amoruso & Urgesi [13]; Amoruso et al. [14,15]; cf. also Amoruso et al. [16]).

In summary, while observing the movements of conspecifics, human beings rely on at least two sources of information. On the one hand, the invariant kinematic attributes which characterize both the actor's and the observer's motor repertoire – thoroughly described in the previous section – are progressively gathered as the observed actions unfold. Given the interdependency of such kinematic invariants, they likely provide with a continuous bottom-up flow of (visual) information which evolves and accumulates over time. On the other hand, contextual information inherent to the physical and social environment in which the actions are taking place allows the observer to make top-down

predictions concerning the actor's goal(s). Such top-down beliefs (intended in a Bayesian sense, see section 3.2) on what goal-directed behaviors are more likely to take place within a given environmental context are complemented by and integrated with the strong prior knowledge of the invariants characterizing human kinematics, derived by the lifelong experience with both performed and observed movements.

These processes – bottom-up evidence accumulation and top-down prediction – unfold online and in parallel, and their interplay eventually provides with the most likely interpretation of the observed action. How such an integration is actually performed likely depends on how reliable the available sources of information are weighted. On the one hand, the invariant kinematic attributes may be abundant and eloquent enough either because the movement is over-trained (e.g., see Manera et al. [210]; Scorolli et al. [290]; Cavallo et al. [55]; Koul et al. [191]) or because the actor proactively shapes his/her own kinematics to facilitate the observer in an interactive context [249,250,329]. In such a scenario, the observer might rapidly and successfully match the accumulating bottom-up visual information with the top-down kinematic priors, and this match could be so compelling to even override other ambiguous or incongruent contextual information (e.g., see Ambrosini et al. [12]; Koul et al. [191]). On the other hand, the actor's movement may not provide with sufficiently reliable information, for instance when it does not belong to the observer's motor repertoire [3,4,300,2,7,334,160,230,331], when the sensorimotor strategy adopted by the actor is poorly predictable (e.g., see Koul et al. [189]) or, more simply, when visual information is poor [67], insufficient [239] or ambiguous [96,315]. In this case, top-down contextual priors could effectively take over the inferential process and make up for the limited kinematic information [17,13–15].

3. Internal models across motor control and action observation

So far, we have reviewed a large body of evidence indicating the prominence of kinematic invariants in motor control. Furthermore, we discussed how the same kinematic invariants can be exploited during the recognition of the actions performed by others. This raises the question of how exactly the brain reuses invariants across motor execution and action observation. Here, we argue that this is possible because the brain forms internal models for motor control and exploits them during action observation and, more broadly, action simulation. We firstly discuss the notion of internal models and then suggest the speculative hypothesis that it is precisely the existence of kinematic invariants that licenses (and perhaps directly triggers) the use of internal models for motor control during action observation tasks.

"*If the organism carries a 'small-scale model' of external reality and of its own possible actions within its head, it is able to try out various alternatives, conclude which is the best of them, react to future situations before they arise, utilise the knowledge of past events in dealing with the present and future, and in every way to react in a much fuller, safer, and more competent manner to the emergencies which face it.*". These lines, written in 1943 by the Scottish philosopher and psychologist Kenneth Craik [68, p. 61] in his essay "*The Nature of Explanation*", represent perhaps the first explicit postulate for the existence of internal models of the world, as well as for their biological role. Although his tragic and premature departure two years later prevented Craik to develop these insights further, his assumptions have been widely supported and expanded in the neuroscientific research starting from the second half of the '80s up to the present time.

3.1. Forward internal models and motor prediction

The neuroscientific investigation of internal models first emerged consistently in the literature concerning computational motor control, which uses approaches derived from engineering and, more specifically, the mathematical framework provided by optimal control theory (for a review see Todorov [318]), to address how movements are planned and performed.

In general, internal models are theoretical constructs that are supposed to mimic the behavior of a natural process [361,223,357]. From the perspective of computational motor control, internal models are representations generated by the nervous system, used to account for the properties of the motor apparatus (e.g., limbs lengths and masses, joint angles) and the environment (e.g., objects features) (Mussa-Ivaldi [231]; Bizzi et al. [41]; Grush [127,128]; Wolpert et al. [359]). Such representations encode the sensorimotor transformations that, starting from these properties, generate the motor commands required to perform a desired movement [235,23,195,307]. As already outlined in several reviews (e.g., see Miall & Wolpert [223]; Wolpert et al. [362]; Mussa-Ivaldi [231]; Wolpert & Ghahramani [356]; Grush [127]),

a first relevant distinction is that between inverse and forward models. Being the former inherently concerned with the *control* side of motor performance (see Neilson et al. [235]; Shadmehr & Mussa-Ivaldi [296]; Imamizu et al. [161]; for a review, see Atkeson [23]), they will not be described further in the present work. Conversely, the latter deal with the *prediction* part of motor control [99] and, therefore, are particularly relevant to the topic at hand.

Forward models – also termed 'predictors' (e.g., see Wolpert & Ghahramani [356]) or 'emulators' (e.g., see Grush [127]) – encode the causal relationship occurring between actions and their outcomes [357,231,119,307], allowing to predict the future state of the motor system and the environment [171,172,195,362,356,127] in terms of expected sensory consequences of actions [99,66]. To do so, a forward model receives as input an *efference* (or *efferent*) *copy* [347,92,139,359] of the outgoing motor command, a concept which was first theorized in 1867 by the German scientist Hermann L. F. von Helmholtz (1867, cited in Gielen [120]), and generates an internal sensory signal, or *corollary discharge* (Sperry [306]; Bell et al. [30]; for a review, see Matthews [214]) as output [223,252].

In light of this, it has been proposed that using forward models could be advantageous for sensorimotor control in at least five ways [361,298]. First, forward model could support the anticipation and suppression of the sensory effects of a movement, or *reafferences*. This allows minimizing the neural responses to predicted sensory features, therefore permitting to enhance more relevant information [30,223,356]. Second, forward models could support the prediction of action outcomes before any actual feedback becomes available. This would permit overcoming the intrinsic noise and delays in sensorimotor loops, which often make feedback-based motor control inaccurate and/or too slow [362,231,356,119,307,66]. Third, "chaining" multiple predictions generated by the forward model while external stimuli and motor outputs are suppressed affords a form of mental simulation of future outcomes, which could be useful for goal-directed planning and imagination [356,127]. Fourth, forward models could support the transformation of errors between predicted and actual outcomes in the sensory domain into corresponding prediction errors in the motor domain, hence providing for appropriate motor learning signals [171,172,223,362,357,99,307,66]. Fifth, forward models can support state estimation, by combining the next state prediction with reafferent sensory corrections for accurate motor control [362,357].

Besides the sensorimotor domain, forward models can be generalized to several cognitive domains depending on the behaviors that are represented, by embedding knowledge of a given environmental property in order to predict future states of the external world [223,362]. These estimates provide a framework for interpreting sensory inputs, allow for anticipating and minimizing processing conflicts and are subject to modification on the basis of sensory information [127,66,252]. Therefore, forward models embed features of natural processes which may involve either the body, the environment or their mutual interactions [359].

3.2. Bayesian interpretations of the idea of internal models

The large body of work on internal models reviewed so far sits well within a broader perspective of the brain as an inferential machine, known as the Bayesian brain hypothesis (Friston et al. [108]; Kappel et al. [178]; for opinion and perspective articles see Knill & Pouget [184]; Clark [60]; Meyniel et al. [221]; for reviews see Friston [107]; Pouget et al. [256]; for further readings see Rao et al. [263]; Doya et al. [84]; McNamee & Wolpert [218]). The basis of this interpretation relies on a theorem that was proposed in 1761 by the English mathematician Thomas Bayes and which, given two random variables x, a model variable (our hypothesis), and y, an observed variable (our data), that are not statistically independent from each other, derives the relation between their respective distributions / densities (for discrete / continuous variables, respectively) with the following equation:

$$p(x \mid y) = \frac{p(y \mid x)\ p(x)}{p(y)} \tag{6}$$

where $p(x \mid y) = $ *posterior probability* (of the model variable x after an observation of the variable y), $p(y \mid x) = $ *generative model* or *likelihood* (of an observation of the variable y, assuming that the hypothesis x is correct), $p(x) = $ *prior probability* (of the model variable x, independently of any observation of the variable y), and $p(y) = $ *marginal probability* (of making an observation of the variable y, used as a normalization factor). In words, equation (6) formalizes how the *belief* of a certain hypothesis should be updated according to how accurately that same hypothesis predicted the observed data (for further readings see Doya & Ishii. [83]; Shadmehr & Mussa-Ivaldi [297], chap. 5).

By applying such statistical framework in neuroscience, the Bayesian brain hypothesis suggests that neural circuits encode and compute probabilities to represent and process sensory information [113,186,221]. Because environmen-

tal events occur simultaneously in a seemingly chaotical way and their observation – if not wrong [27] – is noisy and often ambiguous [93], this probabilistic inferential processing must rely on prior knowledge about event occurrence [206,260]. Such priors are derived by encoding the statistics of the environmental properties [121,155] and undergo a continuous experience-based reshaping during the life of an individual [260]. These updating mechanisms are possible by comparing the internal forward representation of the posterior probability distribution of an event with the actually observed environmental distribution of that same event [121]. Therefore, the Bayesian interpretation provides a useful mathematical framework within which formalizing the notion of 'prediction error', which is computed by the sensorimotor system and used to refine forward models [356,298,359]. Such probabilistic inferences ultimately allow animals to perform decision-making processes in – approximately (see Acerbi et al. [5]) – Bayes-optimal ways [187,188,206,107,358,260].

One recent evolution of the Bayesian brain hypothesis is the active inference framework, which assumes that both perception and action processes in the brain can be described in terms of an approximation to Bayesian inference: the minimization of (variational) free energy [105,251,247]. At difference with the theories of motor control reviewed above, active inference assumes that the brain only needs forward models, but dispenses with inverse models – or better, it only uses a much simpler kind of inverse model compared to what assumed by classical theories of motor control (for a side-by-side comparison of the notions of internal models in active inference and optimal control theory see Friston [106]).

Despite their differences, all the formal accounts of motor control based on some form of Bayesian inference would assume that the brain encodes statistical regularities and invariants in its internal models – perhaps as priors that reflect the "natural statistics" of visual or auditory scenes, or sensorimotor contingencies – and uses them during perceptual processes, such as action prediction and recognition. In keeping, several works have successfully modeled sensory [209,121], decision-making [186,110,204] as well as motor [187,188,359] processes in humans according to a Bayesian perspective. Similar findings supporting (near-)optimal behaviors in non-human primates [333] and other animals (e.g., see Rich et al. [264]) have been provided as well, extending the Bayesian tenets to a broader biological context [221]. As it might be expected, a very consistent environmental attribute encoded by the prior will result in a smaller error between the predicted posterior probability and the actual observation of the event and, as a consequence, will determine a closer to optimal behavior: This is, for example, the case of priors concerning the source of (natural) illumination (assumed to come from above; see Sun & Perona [310]; Mamassian & Goutcher [209]), as well as the cardinal orientation of a visual scene [121].

Therefore, it should be expected that a robust invariant characterizing the environment could represent a benchmark paradigm to test the reliability of an internal model. Indeed, an environmental attribute which is highly consistent in its strength and ubiquity would likely lead to a near-null prediction error, i.e. to a negligible difference between the estimated posterior probability and its current observation. A conspicuous amount of empirical data indicates that, among all the existing environmental invariants, gravitational acceleration best exemplifies the case of internal models, which lead to Bayes-optimal behaviors. Hence, below we discuss empirical evidence that the brain internal models might encode gravity, as a compelling example of the fact that they might encode statistical invariants at large.

3.3. Gravity is encoded in a robust forward model

The reason why developing a forward model of gravitational acceleration would be advantageous is at least twofold. On the one hand, human beings perform generally poor in the visual discrimination of accelerations, especially during short viewing periods (e.g., see Brouwer et al. [49]; for a review see Zago et al. [375]). The sensorimotor delays that – as already mentioned – inherently affect the inverse models [235,161] must therefore be compensated somehow. On the other hand, by acting on the body mass, gravitational acceleration produces a non-negligible inertia of the effectors [354]. When planning a movement – even a simple one, such as a reaching with the upper limb – this effect has to be anticipated. Starting from the early 2000's, a large set of works has provided evidence in support of an internal model of gravity. Because most of this work has been already extensively discussed in several reviews (e.g., see Zago & Lacquaniti [368,370]; Zago et al. [375]; Bosco et al. [47]; White et al. [354]), what follows will be just a brief summary of the main evidence in this respect.

Empirical findings suggest that, when intercepting an object falling along the vertical axis, predictive temporal estimates reflect an integration between visual cues about its motion and prior knowledge of the gravitational effects [375]. The strongest evidence supporting this view comes from experiments performed in the absence of gravity:

During space – or parabolic (training) – flights, astronauts intercepting falling objects perform overly anticipatory movements, which are subsequently interrupted or inverted in direction (McIntyre et al. [217]; Senot et al. [293]; for a review see McIntyre et al. [216]). In such a unique condition, it seems therefore that fast, feedforward-planned, interceptions undergo an important feedback-based error-correcting phase as soon as the violation of the expected gravitational effects is detected. In addition, the kinematics of the upper limb shows adjustments consistent with the hypothesis that the sensorimotor system takes into account the action that gravity exerts on the motor effectors [241, 354]. Experiments on Earth, performed on both human beings and non-human primates, shed further light on this latter phenomenon and suggest the existence of an effort-optimization strategy which relies on effective motor plans (i.e. that take into account the gravitational effects) to minimize muscles effort (e.g., see Poirier et al. [254]; Gaveau et al. [115]). Other studies have further disentangled the anticipatory processes involved in the interceptive behaviors by addressing the time-to-contact estimation and interception of falling objects in both vertical [371,292] and projectile [46,78] motions or for objects rolling down an inclined plane (La Scaleia et al. [193]; Mijatović et al. [227]), and extended the investigation to other more complex interceptive actions, such as batting movements (e.g., see Katsumata & Russell [179]) and object manipulation (e.g., see Toma et al. [320]). Overall, these results show that interceptive performance is largely more accurate and precise for 'naturally' falling objects compared to experimentally manipulated velocity profiles violating gravity (e.g., inverted or doubled gravitational acceleration, constant velocity, etc.; see Zago et al. [373]; Bosco et al. [46]). In general, the pattern of errors indicates a predominance of predictive mechanisms consistent with spatial and temporal estimates relying on the expectation of the gravitational effects [47,194].

Rather than reflecting an accurate internalization of the Newtonian principles of gravity, these predictions likely represent a naïve, i.e. only approximately correct, heuristic of the physical laws (Ceccarelli et al. [56]; for a review see Hubbard [159]). Nevertheless, the encoding of this robust environmental invariant starts early in life and gives rise to a highly reliable internal model allowing for an immediate perception of its violations [305]. Once learned, the extreme robustness and ubiquity of this invariant would only afford, if anything, a negligible experience-based tuning of the corresponding internal model – a noteworthy difference from the error-correcting process which continuously reshapes other priors during the life of an individual (e.g., as elucidated by the size-weight illusion affecting object manipulation; see Flanagan & Beltzner [97]). Since prediction errors would therefore result almost entirely from environmental and/or sensorimotor noise, unexpected violations of gravitational effects can be detected unusually fast and, by the same token, might be rather challenging to compensate for [217,354], leading to an adaptation of the preexistent model itself rather than to the creation of another internal representation *ex novo* (Zago et al. [371, 372]; Zago & Lacquaniti [369]; Bosco et al. [46]; Hubbard [159]). Altogether, these findings indicate that gravity is internalized as a particularly robust Bayesian prior (MacNeilage et al. [208]; Alberts et al. [9]; Jörges & López-Moliner [173,174]; see also Shadmehr & Mussa-Ivaldi [297], chap. 5) with clear consequences on sensorimotor behavior.

3.4. Summary and speculative proposal

In this section, we discussed the widespread idea that the brain might learn and use internal models for perception and motor control (and more broadly, for several facets of cognitive processing) and then we reviewed empirical evidence suggesting that internal models could encode robust environmental invariants, such as gravity. Clearly, if the main role of generative models is learning about (and simulating or emulating) statistical regularities, their contribution should not be restricted to gravity, but also to other invariants that we encounter (or produce) constantly – including the kinematic invariants that have been the focus of this article. Interestingly, if we assume that internal models for movement control encode kinematic invariants and that they can be reused for action perception (and imagination), then the consequence is that our internal models should make us exquisitely sensitive to perceiving the same kinematic invariants that we use during movement. Crucially, because kinematic invariants are (by definition) the most stable traits of our movements, they should be also the most stable information that we are able to perceive and decode during action observation.

This leads to the speculative proposal that the main contribution of the motor system (and of its internal models) to action observation is to process kinematic invariants, as these are the most salient and stable characteristics of observed movements. If this hypothesis is correct, then the presence (or the expectation) of kinematic invariants could be sufficient – and perhaps necessary – to engage internal models for the control of movement during action observation; whereas the same models would not be engaged (or engaged to a significantly lower extent) during the processing of perceptual streams that lack kinematic invariants. While this is clearly a speculative proposal, it could

help conceptualizing the large body of evidence described in this paper about the importance of motor invariants during action observation.

Potentially, the models capacity to process kinematic invariants could serve multiple roles, such as inferring / predicting biological movements and their underlying intentions (action prediction and intention recognition), guiding attention towards the kinematic features of movement that are expected to be more informative (hypothesis testing) and finessing one's movements to be more informative for co-actors (sensorimotor communication). All these (and other) capabilities have been linked to the functioning of internal models in a way or another. Future research is needed to establish whether it is specifically the capability to process motor invariants that renders internal models so useful.

Finally, if the above hypotheses are correct, it could be possible to reconsider neurophysiological evidence of motor activation during action observation as the brain's inference of kinematic invariants of movement and the subsequent exploitation of these invariants to infer the actions and intentions of our conspecifics, as well as forming social (cooperative and competitive) plans. The rationale of this idea is that while non-motor systems (e.g., the visual system) can robustly learn and process information about the statistics of movements, the motor system is especially well suited to pick up kinematic invariants – as it is already tuned to such invariants for the sake of motor control. Testing this idea would require systematically varying the amount (and reliability) of kinematic and other invariants during movement perception and testing whether the motor system plays a privileged role (or perhaps a causal role, by using inactivations) when motor invariants are key.

4. Conclusions

The present review piece was aimed at presenting, within a unified framework and in a single place, an extensive description of all human motor invariants so far consolidated in literature. That of invariants in motor behavior is certainly an old-fashioned concept that is substantiated by plenty of evidences, which however are often overlooked in recent studies that either rediscover old results or worse, collide with basic knowledge about how movement is generated, organized and planned. A better understanding of motor invariants also offers a robust theoretical and empirical ground for the investigation of higher-order phenomena such as interpersonal coordination, sensorimotor communication, action perception or intention decoding. In fact, motor invariants are a set of measurable objective properties of movement, most often the only true observable in behavior. Invariants are indeed the only thing we can use to reverse engineer the properties and functions of internal models which is instead a purely speculative construct. Interestingly, motor invariants are not only measurable by experimenters in their lab but can actually be read and used by conspecifics during real life. Here, transitioning from an empirical to a theoretical ground, movement invariants (and variations upon them) constitute the only shared informational medium between animals, given that language is a relatively recent acquisition in evolution. This basic fact alone should lead to acknowledge this framework as the only meaningful one when approaching the investigation of social interaction. Rather, social interaction is often investigated as if human beings, i.e. "special" animals, had developed highly sophisticated cognitive abilities by losing such a primitive sensorimotor communicative function in favor of abstract or symbolic thinking. Well, we should not be so optimistic about us being so different from animals.

Nevertheless, it should be straightforward to accept that, given the existence of motor invariants, any Darwinian agent should be sensitive to these regularities in conspecifics' behavior. In fact, motor invariants not only save us time and resources when making top-down directed inferences but actually contribute to make up a social saliency map whereby certain spatiotemporal spots are destined to attract our best efforts. Biological motion invariants (i.e. Fitts' law, bell-shaped velocity profile or the 2/3 power law) isolate "humans" (or animals) from the background. Maximal finger aperture or the end state comfort, willingly or not, project human intentions outside their own body right before they are needed to our conspecifics to read and exploit them appropriately. Finally, it is worth mentioning that all of these features are visual in nature but are inherently constrained by biomechanical and neuromotor principles. Considering that such principles are intrinsically present in action planning and execution, our claim is that the internalized knowledge of how inertia, gravity, the viscoelastic properties of muscles or how the force-contraction coupling for muscle recruitment (and so on) works, constitutes the most basic set of Bayesian priors available in support of others' actions classification and prediction. When motor neurophysiologists discuss motor theories of perception, they should have this in mind, certainly not the demonstration that BA4 or BA6 is active in an fMRI action observation study. The motor system is far more than that, and we should not forget that Nature has solved these biomechanical problems since we crawled out of water; For millions of years, expressing motor invariants – and being able to read

them in others – probably made the difference in terms of survival, mating and feeding opportunities within a species hallmarked by its social life. To make sense of this, we advanced the speculative hypothesis that the main contribution of the motor system – and its internal models – during action observation could be processing stable kinematic invariants. This hypothesis, which remains to be tested in future studies, points towards the centrality of kinematic invariants not just for action generation, but also to engage the brain internal models in sophisticated social cognition.

Declaration of competing interest

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