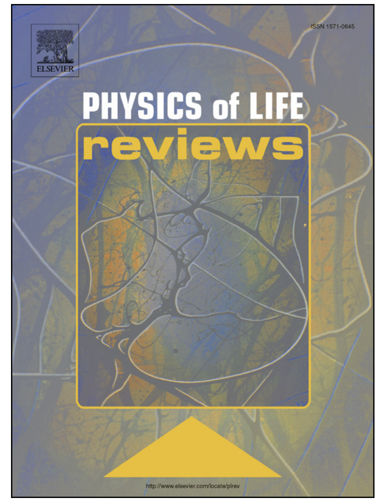

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The complementarity of 'Muscleless' motor synergies with motor control strategies in humans and robots: Reply to comments on "*Muscleless* motor synergies and actions *without movements*: From motor neuroscience to cognitive robotics"

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One of the basic assumptions of this study is that the motor synergies recruited for overt and covert movements are both the result of the animation of an internal body schema. One may wonder how accurate such internal model needs to be and, in this respect, we agree with the observation in the commentary by Ptak R (2019) that "a good theory of simulation should specify the necessary biological constraints of an action production system, be it involved in overt action, action simulation, or both." Even if the body schema is muscle-less it does incorporate critical biological constraints that are essential for the generation of biologically plausible motions, such as the limited range of motion of the different articulations, the basic timing or tempo of covert action sequences, or the stability constraint of synergy formation in whole body reaching (Morasso et al, 2010). The effectiveness of techniques for the mental rehearsal of actions, as in downhill skiing, also suggests that some kind of reinforcement learning supports the consolidation of most rewarding memory trace of the action that is ready to be executed in the real world.

A related question, that was not specifically addressed in the review, is the set of control mechanisms that ultimately transform muscleless motor synergies into coordinated muscle activation patterns. Synergy formation and motor control are indeed two different although interrelated processes with different computational mechanisms. The former process is like the musical score of a symphony that prescribes the recruitment of different instrumental groups, the basic timing, the melodic line, as well as qualitative notations as "andante con moto" or "fortissimo" that are intended to modulate the actual performance. However, such real execution of the score involves the individual musicians and the director in such a way to fine-tune the detailed texture of the sound, also taking into account the physical and social environment in which the performance is taking place.

Motor control is a process that involves the brain, the muscles, the skeleton, the exteroceptive and proprioceptive sensory channels, and the environment, by using three main types of control strategies, combined in different ways according to the task: feedforward control, feedback control, and stiffness control (Chinnelato, E, 2019). Feedforward control is the control strategy more closely associated with the muscleless synergy formation process advocated in this review. For example, in whole body reaching we may hypothesize that the generated kinematic patterns also include a prediction of the gravity-dependent destabilizing torques that need to be compensated for each postural configuration of the body: it only requires that the internal body schema includes some knowledge of the distribution of masses in the different body segments. However, feedforward control patterns may be insufficient for the success of a purposive action for two main reasons: insufficient accuracy and potential instability of specific body postures, such as the upright standing posture. Inaccuracies of the body model, in addition to sensory and motor noise, as well as unaccounted environmental disturbances are unavoidable sources of imprecision of the actions driven by feedforward control patterns. Closed loop feedback control, based on suitable sensory error signals, is one of the universal control paradigms for compensating the sources of imprecision above. However, tuning the control parameters or gains is a critical adaptation process that must trade-off contrasting requirements: precision, that advocates high values of the gains, with stability, that imposes strict upper bounds of such values. The challenge for an effective feedback compensation is attenuated if it can operate on top of a sufficiently accurate feedforward compensation; however there is an intrinsic limit to the capability of the feedback control paradigm due to the delay of feedback error signals. By itself this is a strong potential source of instability of the control loop and the problem is further exacerbated if the task is intrisically unstable, such as the maintenance of bipedal or monopedal upright posture.

On the other hand, the muscle stiffness strategy operates by modulating the degree of coactivation of antagonistic muscles groups and carries out a similar function of compensating for unaccounted disturbances/inaccuracies with an intrinsic and un-delayed feedback action related to the visco-elastic properties of muscles. However, it has limitations, for example in terms of muscle fatigue and physical arrangements of skeletal muscles and tendons. Whole body reaching, with the underlying task of maintaining the upright bipedal posture, is indeed a good example of the hybrid integration of different control paradigms that is evoked when a covert whole body reaching action is translated into the corresponding overt action. The muscleless synergy is formulated as a combination of a virtual force field applied to the hands, expressing the focal component of the task, and a force field applied to the pelvis, expressing the associated postural component, aimed at keeping the projection of the body center of mass inside the bipedal support area (Morasso et al, 2010).

From such synergy the feedforward controller can predict the baseline of muscle activation that, at least approximately, is needed to compensate the gravity pull, thus implementing a sort of static stabilization of the body motion. However, even if perfectly tuned, such static compensation is insufficient to achieve dynamic stability because upright standing, as a kind of inverted pendulum, is intrinsically unstable, with a saddle-like instability. The dynamic part of the stabilization process is carried out, in part, by the stiffness strategy and, for the remaining part, by a delayed sensory feedback strategy. It was demonstrated indeed that a pure stiffness strategy is impossible for physical/biological reasons (Casadio et al., 2005; Loram and Lakie, 2002) and there is ground to believe that the feedback strategy, in this case, can be characterized as "intermittent" (Bottaro et al, 2008; Asai et al, 2009). Such intermittent control policy exploits an "affordance" provided by the saddle-like instability of the inverted pendulum model, namely the existence in the phase plane of the inverted pendulum (angular tilt away from the unstable equilibrium vs angular velocity) of an unstable and a stable manifold. During postural oscillations around the unstable equilibrium the intermittent control policy alternates off-phases and on-phases, namely it switches off dynamic active control if the state of the inverted pendulum (evaluated via delayed sensory feedback) is closer to the stable than to the unstable manifold, because in this case the dynamics of the inverted pendulum is providing for free an intrinsic stabilization effect, and it switches it on, with a simple proportional/derivative control action, in the opposite case. It is important to highlight that the target of the on-phase is not the equilibrium point in the phase plane but the whole stable manifold: the alternation of on-phases and off-phases does not provide asymptotic stability but a much more robust form of bounded stability, around a limit cycle. In short, during the transition from covert to overt actions the muscleless motor synergies evoke in a natural and seamless manner the different control mechanisms summarized above, while keeping the overall coordinated structure and tempo of the action. Moreover, the issue raised by the intermittent control policy above is an example of exploiting the ecological background of an action, namely the integration in the control policy of the dynamic interaction of the body with the environment.

We would like to stress the separation but also the deep complementarity between synergy formation and motor control. Intermittency, for example, characterizes the latter but not the former computational process. In whole body reaching, from an initial equilibrium posture to a final equilibrium posture, the synergy formation process, that distributes the action to the redundant set of degrees of freedom of the body, incorporates the constraint of static equilibrium but the actual dynamic stabilization of the initial and final postures is carried out by a different mechanism that exploits muscle stiffness and intermittent feedback control. Friston and Parr (2019) point out to the intriguing concept of 'Strange Inversion' that implies 'desired movements causing motor commands' and the inverse, the consequence of which has computational implications in the context of dissolving many complex problems in traditional optimal control and forward-inverse model formulations (Friston, 2011). At the same time, the body schema framework also allows a feasible way to simulate 'desired movements' of others and anticipate others actions/intentions (as if one self was acting). Vernon (2019) in his commentary has taken this paradigm even forward with the intriguing idea of combining such action simulation with episodic memory (that we correctly have not gone into details in our review) to look at a more general framework for internal simulation in cognitive agents (and how to endow this capability in robots). This has implications in human robot symbiosis (Sandini et al, 2018) with applications in many directions.

Sternad and Hogan (2019) correctly point out that most of the examples and considerations of the review article, focused on the biological plausibility of internal action simulation based on attractor dynamics of force fields analogous to the equilibrium-point hypothesis, is mostly confined to quasi-static point to point reaching actions. However, this formulation can be easily extended to more complex paradigms where the apparent continuity and smoothness of the visible (or audible) trace can be explained as a sequence of overlapped sub-actions: consider the case of cursive handwriting (Morasso et al, 1983), hand drawing (Mohan et al 2011) or connected speech (Sanguineti et al, 1998). An apparently different ballgame is related to rhythmic movements that are typically characterized by attractor dynamics to limit cycles rather than to fixed points. However, we already observed how the two different dynamic paradigms can coexist in the same action, say whole body reaching movements, covering different aspects of the action, namely the reaching synergy and the dynamic stabilization via intermittent control. Moreover the same approach can be applied to typically rhythmic movements like locomotion (Fu et al, 2014), thus combining in the same process the goal of stability, compensating the destabilizing effect of gravity, with the goal of rhythmicity, typically expressed in terms of central pattern generators. As observed by Sternad & Hogan, muscle stiffness is certainly a key element in this kind of interactive actions that needs to be matched to the dynamic constraints of the environment, according to general principles of ecologic adaptation.

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Declaration of interests

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

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: