THE NEXT STEP IN DEVELOPMENTAL EMBODIMENT RESEARCH: INTEGRATING CONCEPTS AND METHODS

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THE NEXT STEP IN DEVELOPMENTAL EMBODIMENT RESEARCH: INTEGRATING CONCEPTS AND METHODS

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Table of Contents

1. THEORETICAL PERSPECTIVES ON DEVELOPMENTAL EMBODIMENT RESEARCH

2. METHODOLOGICAL ACCOUNTS FOR A DEVELOPMENTAL EMBODIMENT PERSPECTIVE

3. DEVELOPMENTAL EMBODIMENT RESEARCH: EMPIRICAL STUDIES

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Editorial: The Next Step in Developmental Embodiment Research: Integrating Concepts and Methods

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Editorial on the Research Topic

The Next Step in Developmental Embodiment Research: Integrating Concepts and Methods

INTRODUCTION

Embodiment has become a key concept in human life sciences, and specifically in the study of the human mind. The question, how to integrate a developmental perspective with embodiment research, has recently emerged in cognitive science (Maruyama et al., 2014; Nava et al., 2018; Marmeleira and Duarte Santos, 2019), developmental psychology (Marshall, 2014; Gredebäck and Falck-Ytter, 2015), language processing studies (Dove, 2018), and robotics (Gordon, 2019; Kuniyoshi, 2019). In addition, calls for expanding the timeframe of developmental processes under study beyond early childhood to the lifespan are voiced (Loeffler et al., 2016; Reed et al., 2019). However, these first attempts emerged separately in each of their respective fields.

The aim of this Research Topic was to overcome this divide by inviting theoretical and empirical contributions targeting the developmental dynamics of embodiment phenomena across a broad range of disciplines. We invited contributions that discuss different timescales of developmental dynamics—from sensitive periods to across the lifespan, intergenerational, and longer-scale evolutionary perspectives—along with contributions that target different system levels—from epigenetics to complex motor behavior.

THEORETICAL PERSPECTIVES ON DEVELOPMENTAL EMBODIMENT RESEARCH

In a thematic review, Lux et al. propose to integrate embodiment approaches from a developmental perspective. They distinguish between two lines of embodiment approaches: environmental approaches which focus on the biological embedding of experiences, specifically in sensitive periods of development, and agency approaches, which emphasize the role of embodiment in active interaction with the environment. In addition, they outline different levels of embodiment, related data modalities, and the timescales for which developmental embodiment research needs to account. They argue that the study of embodiment phenomena needs to be function-specific, cross-level, and accounting for the different timescales of developmental processes thus implying an interdisciplinary approach.

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In his opinion paper, Lickliter critically examines the proposal by Lux et al. and highlights two important issues for developmental embodiment research: First, from a developmental perspective, the mechanisms and dynamics which bring about phenotypic stability and phenotypic variability are the same. Studying them in the context of an individual's active engagement with the environment allows one to pinpoint change and stability along the specific developmental trajectory. Second, embodiment opens up and at the same time constrains possible developmental outcomes, but this opening-up and constraint is itself a result of development. Thus, a developmental perspective clearly illuminates the mechanisms underlying embodiment phenomena, but at the same time points to the complexity of this interdisciplinary endeavor.

Coming from the perspective of developmental science, Marshall et al. argue that an integration of developmental and embodiment research needs to account for three different epistemological states of the body: the body as biological organism, addressed by phylo- and ontogenetic developmental theories, the body as medium for the interaction with the environment, which emphasizes an interactionist and co-constructivist approach, and the body as lived experience, which points toward the integration of phenomenological accounts. They advocate for placing the study of organization and systems in the center of developmental science and adapting the metatheoretical framework of process-relational developmental systems theory (e.g., Overton and Lerner, 2014).

While these articles highlight the interdisciplinarity of developmental embodiment research, Mille et al. outline the potential within a specific research field: the study of cognitive changes associated with aging. They explore how age-related changes in the neurophysiological substrates underpinning perceptual and memory interactions in older adults could explain the more broad cognitive changes associated with aging in terms of gains and losses.

METHODOLOGICAL ACCOUNTS FOR A DEVELOPMENTAL EMBODIMENT PERSPECTIVE

Another set of contributions introduce new experimental paradigms to study the interrelatedness of embodiment and development or re-interpret existing paradigms, data, and methods from a developmental embodiment perspective.

In their thematic review, Sen and Gredebäck introduce an embodied account for the "mobile paradigm" (Rovee and Rovee, 1969; Rovee-Collier, 1995), a well-established approach to study the development of memory skills through operant conditioning of simple motor behavior in infants. According to Sen and Gredebäck, an embodied account of the mobile paradigm accounts for the individual sensorimotor experiences—and importantly their interindividual variance—gained from the motor interaction with the environment. Thus, this approach would be more powerful in comprehensively explaining developmental changes in cognitive and motor functions.

Similarly, Musculus et al. advocate for an embodied approach for the investigation of developmental changes in action planning across the lifespan. Based on an in-depth review of research on motor and cognitive planning, they argue that cognitive development is fundamentally driven and constrained by motor development and needs to be studied in an integrated manner. For this, they propose the integrative concept of "embodied planning" and introduce a novel climbing paradigm to study action planning from a developmental embodiment perspective.

In their contribution, Riva et al. propose a new therapeutic method, "Regenerative Virtual Therapy," to investigate and intervene in the dynamics of a faulty bodily self-consciousness underlying mental disorders. Using a Bayesian modeling approach, they suggest combining mindful attention, cognitive reappraisal, and brain stimulation techniques with rewarding multisensory bodily experiences may overwrite faulty bodily experiences and regenerate wellbeing.

DEVELOPMENTAL EMBODIMENT RESEARCH: EMPIRICAL STUDIES

Five articles contribute original research studying different levels of embodiment from a developmental perspective. Reggin et al. investigated abstract word acquisition from a linguistic developmental perspective and found partial support for the affective embodiment account: Word valence, interoception, and mouth action facilitated abstract word acquisition more than concrete word acquisition. They conclude that affective embodiment is important to children's acquisition of abstract words, but that there is considerable variance to be accounted for by other factors such as contextual diversity of vocabulary use. Wienecke et al. tested whether a combination of basketball training and mathematics improves motivation for classroom-based mathematics in school children. Their findings indicate that learning mathematics in combination with physical activity increases intrinsic motivation levels while the underlying processes still warrant future investigations.

In contrast to these studies, Amico and Schaefer report findings that walking toward the target during a visual-spatial working memory task impaired encoding and recall performance across age groups. Their results clearly contradict earlier studies in the field of cognitive embodiment and, thus, support the notion that embodiment processes are highly functional specific.

Finally, two papers present research conducted in populations of particular interest for developmental embodiment research: highly functional adults and vulnerable groups. Stadler et al. studied shared action representations in Taekwondo experts and novices using video-based evaluations of complex movement sequences. They show significantly more overlap within the expert group as compared to the control group. They conclude that experts might benefit from sensorimotor skills to simulate the observed actions more precisely and that this enhances shared representations. Clausing and Non investigated whether immigration-related stress impacts the cardiometabolic risk and epigenetic markers of Latinx immigrant mothers and their children, integrating a cross-level approach with an intergenerational perspective. They found associations of stress markers with cardiometabolic risk and, to a smaller degree, with epigenetic markers indicating that the life circumstances of immigrant families can become biologically embedded in both adults and children, and that DNA methylation may be on the pathway linking stress with cardiometabolic risk.

CONCLUSION

Overall, the contributions highlight the growing relevance and potential of developmental embodiment research. In some cases, this approach allowed integration of contradictory findings, in others it challenged existing knowledge or opened-up new research avenues. Also, the framework requires methodological innovations which explicitly target cross-level dependencies—some of which are presented here. The research articles presented in this special issue highlight the value of such cross-level examinations and the potential of focusing on sensitive periods, comparisons across the lifespan, and specific populations to further elucidate the developmental dynamics of embodiment processes. Developmental embodiment research has clearly taken the next step.

AUTHOR CONTRIBUTIONS

VL and MK drafted the first version of the manuscript. All authors contributed to, commented on previous versions of the manuscript, read, and approved the final manuscript.

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REVIEW
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A Developmental Framework for Embodiment Research: The Next Step Toward Integrating Concepts and Methods

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Embodiment research is at a turning point. There is an increasing amount of data and studies investigating embodiment phenomena and their role in mental processing and functions from across a wide range of disciplines and theoretical schools within the life sciences. However, the integration of behavioral data with data from different biological levels is challenging for the involved research fields such as movement psychology, social and developmental neuroscience, computational psychosomatics, social and behavioral epigenetics, human-centered robotics, and many more. This highlights the need for an interdisciplinary framework of embodiment research. In addition, there is a growing need for a cross-disciplinary consensus on level-specific criteria of embodiment. We propose that a developmental perspective on embodiment is able to provide a framework for overcoming such pressing issues, providing analytical tools to link timescales and levels of embodiment specific to the function under study, uncovering the underlying developmental processes, clarifying level-specific embodiment criteria, and providing a matrix and platform to bridge disciplinary boundaries among the involved research fields.

Keywords: embodied experiences, agency approach, environmental approach, developmental systems theory, language acquisition, cognition, perception, interoception

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INTRODUCTION

Embodiment has become a key concept in human life sciences in recent years. Although generally understood as the sum of bodily preconditions of cognition, emotion, and behavior, a closer look unveils that conceptualizations of embodiment vary strongly among research areas and theoretical schools: from embodied simulation to embodied cognition, from biological embedding of experience to interoception and the embodied mind. Differences also include types of knowledge production (e.g., cognitive processing models vs. motor developmental pathways vs. computational simulations of neural activity patterns), data modalities (e.g., self-reports vs. medical diagnoses vs. movement trajectories vs. molecular epigenetic profiles), and the involved levels of analysis (e.g., psychological function vs. gene expression). Different research areas and theoretical schools also account for different timescales across which embodiment processes can be analyzed (e.g., life-time effects vs. acute activation). Importantly, some of the most pressing topics with the greatest potential to advance embodiment research cut across research disciplines and are currently significantly hampered by the lack of a common theoretical framework that bridges the different conceptualizations of embodiment.

The current situation calls for an interdisciplinary conceptualization of embodiment. Here, we propose to adopt a developmental perspective as an integrative cross-disciplinary framework of embodiment research serving three main purposes: A developmental perspective on embodiment *accounts for the different timescales* that underlie the processes of incorporation and expression of an agent's embodied experiences in the interaction with the environment. It also *relates different levels of embodiment to one another* as they develop over the lifespan, based on their biological and functional interconnectedness. Finally, it *clarifies disciplinary boundaries* and finds connection points by identifying transmission hubs between the levels involved in a particular embodiment process which, then, creates links for collaboration between participating disciplines. This is especially important for research areas which try to overcome disciplinary limits but are still bound to the methods and committed to research standards within their respective field. Thus, on the basis of those three purposes, the proposed framework does not aim at providing a new definition of embodiment but shall be understood as a platform and analytical tool to enable and support integrative cross-disciplinary embodiment research by clarifying critical aspects that currently hamper the advance in the field.

In the following, we will, first, characterize two main types of approaches to embodiment in the life sciences, agency and environmental approaches (see section Integrating Environmental and Agency Approaches to Embodiment) and discuss how they conceptualize developmental processes underlying embodiment phenomena (see section Developmental Processes Grounding Embodiment: Implicit and Underexplored). Due to the variety of embodiment research in the life sciences, these two sections do not cover all existing embodiment concepts. We focus on those fields of embodiment research and concepts of embodiment for which adapting an integrative developmental perspective would be most productive from our perspective. Second, we will present examples for the potential and the challenges of developmental embodiment research (see section Developmental Embodiment Research: Cross-Disciplinary Examples). Finally, we discuss our framework of developmental embodiment research in more detail (see section Toward an Integrative Framework for Developmental Embodiment Research).

INTEGRATING ENVIRONMENTAL AND AGENCY APPROACHES TO EMBODIMENT

Developmental embodiment research, as we propose it in this paper, builds on two distinct lines of current embodiment research in the life sciences, which rarely connect conceptually, or in empirical studies (see **Box 1** and **Table 1** for an introduction into key concepts, targeted embodiment phenomena and related key references): First, "*agency approaches*" that emphasize how bodily embeddedness, anatomic preconditions, and physiological as well as neurophysiological foundations momentarily enable movements, actions, and psychological functions. Second, "*environmental approaches*," which describe how the physical, social, and cultural environment is incorporated, and affects the physical structure of the body or brain and subsequently its function. Agency approaches mainly focus on the acute activation and involvement of the body, including basal body functions, signals, resources, and conditions etc. with emphasis on the active interaction with the environment. Research originating from an agency approach investigates how embodied experiences are mobilized and how they influence interactions with the environment. Environmental approaches, in contrast, focus on the long-term impact of environmental signals on bodily preconditions of mental functions and mental health outcomes. Research coming from an environmental approach investigates how environmental (pre)conditions and events are incorporated into the body to become embodied experiences. With our developmental framework, we propose to integrate agency and environmental approaches by understanding the body as a reservoir of experiences, providing a sort of storage and 'memory' of experiences and capabilities necessary for action and mental functions which are activated and mobilized in the specific moment of interaction with the environment.

Other attempts to classify embodiment approaches often distinguish a third group of phenomenological approaches (Overton, 2008), or further differentiate along methods (experiential/objective), epistemological perspective (1st, 2nd, and 3rd third person perspective), and object of research (cognitive structure/practice) (Hornecker et al., 2017). We subsume phenomenological approaches under the group of agency approaches, as these are also primarily concerned with the momentary preconditions of consciousness, action, or perception, although from a first (or second) person perspective.

Integrating agency and environmental approaches to embodiment clearly broadens the notion of embodiment compared to its use in discipline-specific research areas (e.g., in embodied cognition research, see Wilson, 2002). In addition to different neural networks involved, e.g., in decision making, abstract word recognition, and movement execution, embodiment processes also encompass the physical constitution of the body (the anatomic structure of the limbs, homeostatic feedback processes, hormonal balance, basic sensory organization, and function, etc.), the neural networks involved in the regulation of these processes, and the molecular underpinnings of these regulation processes and network constitutions. This broader notion of embodiment further includes the focus on the anatomic structure of the body used in robotics (see Pfeifer and Bongard, 2006), the notion of an extended mind to our immediate environment and, most importantly, intersubjectivity emphasized in phenomenological accounts (see Fuchs, 2017), as well as the biological embedding of experiences across the lifespan (see Rutter, 2012). Still, not all body processes and conditions are of interest for developmental

BOX 1 | Approaches to embodiment in the life sciences which contribute to the proposed developmental perspective.

The rise of embodiment concepts in the life sciences started out in the 1980s, when linguists, cognitive psychologist, and robotic engineers turned to the study of motor and sensory processing, emphasizing that they shape the way our mind works. Neuroscience and philosophy of mind contributed to further advance this perspective (Varela et al., 1991; Gibbs, 2005; Shapiro, 2011). Subsequently, a range of different concepts developed by building up on the joint idea that our bodily preconditions are the foundation for the perception of ourselves (in the sense of consciousness and interoception) and the perception of the environment with which we interact, affecting a range of processes and phenomena related to e.g., cognition, emotion processing, social interaction, aesthetic perception, and mental health. We subsume these as agency approaches to embodiment (see **Table 1**).

While the lines along which different embodiment concepts should be distinguished are still highly debated (for embodied cognition, being the most prominent concept of an agency approach to embodiment, see e.g., Clark, 1999; Wilson, 2002; Overton et al., 2008; Kiverstein, 2012; Meteyard et al., 2012), they were picked up quickly in cognitive psychology and other related fields of research (see **Table 1**). Here, they provided a platform for the use of the newly established neurofunctional approach based on neuroimaging techniques (mainly fMRI) within the existing cognitive paradigm. In sports psychology and movement science, for example, the concepts of embodied cognition and embodied simulation bridged the gap between neurocognitive research and practical knowledge based on motor expertise, movement learning, as well as motor rehabilitation techniques. Further, the acknowledgment of the embeddedness of our mind within our most basal bodily functions via interoceptive pathways (see Craig, 2004, 2009a,b) and their influence on emotion processing, self-awareness, and time perception, strongly influenced research fields such as computational psychiatry and psychosomatics, and mental health research (Petzschner et al., 2017; Khalsa et al., 2018). Here, we already observe first steps to integrate agency approaches to embodiment with those studying processes of incorporation of experiences at several underlying biological levels (Petzschner et al., 2017).

This turn to the bodily preconditions of action, perception, and emotions met with a turn to the body in population health and epidemiological research (see Krieger, 2005; Hertzman, 2012; Rutter, 2012; Gluckman et al., 2016). The question was whether and how adverse or advantageous environmental conditions, experienced during sensitive periods in life (e.g., pre- or perinatal), become incorporated into the body and subsequently constitute divergent developmental pathways of physical and mental health. The concepts used to describe such long-term effects of environmental impacts, which we subsume as environmental approaches to embodiment (see **Table 1**), focus on different physiological levels of the body underlying mental functions, e.g., (psycho)physiological feedback mechanisms, hormone regulation, neural networks, brain anatomy, inflammatory processes, gene-environment interactions, as well as epigenetic mechanisms (e.g., Godfrey et al., 2007; Wadhwa et al., 2009; Danese et al., 2011; Rutter, 2012; Nelson, 2017; Bush et al., 2018; Aristizabal et al., 2019). We limit our discussion here to those studying the impact on mental health. While these concepts differ in their focus on the time-point and duration of the environmental impact, spanning transient to persistent effects, they all attribute a central role to developmental processes in the translation of the environmental impact to later mental health outcome. Thus, the classification of developmental pathways underlying diverse outcomes is a joint important goal in these concepts. It is also assumed necessary for translational research and future intervention (Rutter, 2016).

embodiment research, but only those which participate in the incorporation, shaping, and expression of embodiment experiences, in the context of e.g., a particular mental function or mental health outcome under study. Developmental embodiment research, as we propose it here, provides a matrix and platform through which different approaches of embodiment research can collaborate in the interdisciplinary study of a particular mental function or mental health outcome.

DEVELOPMENTAL PROCESSES GROUNDING EMBODIMENT: IMPLICIT AND UNDEREXPLORED

Although developmental theories are one of the historical pillars of embodiment research (Overton and Lerner, 2012), the question of how embodied functions develop often comes second in empirical studies. Some authors even question that a developmental perspective contributes at all to elucidate the underlying mechanisms of embodiment phenomena (e.g., Körner et al., 2015). In our view, both the agency approaches and the environmental approaches to embodiment imply developmental processes and would therefore profit from an explicit developmental perspective.

Agency approaches, on the one hand, implicitly acknowledge lifespan developmental changes in e.g., cognitive and motor functioning within their theoretical framework, but the specific impact on the embodiment phenomena under study is not empirically investigated. Referencing Gibson's ecological theory (Gibson, 1986//2014) or Piaget's stages of cognitive development (Inhelder and Piaget, 1958; Piaget, 1977), for example, agency approaches emphasize that the mind develops through an individual's interactions with the material world around it. Consequently, (inter-) individual differences in e.g., perception, imagination, language processing, or aesthetic judgement, as well as in neuronal activity measured in the sensorimotor cortex are understood as having evolved from these interactions. The activation of interoceptive and motor processing networks during these higher cognitive tasks then works as an indicator for the degree of bodily groundedness of a function.

Studies of developmental changes of embodiment phenomena based on the agency approach are rare, with exceptions often focusing on action perception and speech development during infancy and early childhood (Wellsby and Pexman, 2014; Gredebäck and Falck-Ytter, 2015; Fuchs, 2016b; Gottwald et al., 2016; Inkster et al., 2016; Gredebäck, 2018; Loucks and Sommerville, 2018). However, a number of studies examines changes of embodiment phenomena on a much shorter timescale due to e.g., training effects, therapeutic interventions, or short-term manipulation and impairment of motor capabilities (e.g., Koch et al., 2008; Marasco et al., 2011; Meugnot et al., 2014; Kuehn et al., 2018). It is likely that the mechanisms underlying short-term plastic changes of embodiment processes overlap with those underlying the longer-term developmental changes (Wenger et al., 2017). To fully bridge these timescales, however, agency approaches need to be integrated with environmental approaches.

TABLE 1 | Examples of agency and environmental approaches to embodiment: concepts, phenomena and fields of research.

Agency approaches		**Environmental approaches**	
Concepts			
Embodied cognition	Wilson, 2002; Leitan and Chaffey, 2014; Shapiro, 2014	Biological embedding of experiences	Danese et al., 2011; Rutter, 2012; Nelson, 2017; Bush et al., 2018; Aristizabal et al., 2019
Embodied simulation	Gallese and Goldman, 1998; Gallese, 2007, 2017, 2019	Developmental Origin of Health and Disease (DOHaD)	Barker, 1995, 1998; Hanson and Gluckman, 2008; Gluckman et al., 2016
Somatic marker hypothesis	Damasio, 1994, 1996	Environmental epigenetics	Weaver et al., 2004; Zhang and Meaney, 2009; Bollati and Baccarelli, 2010
Inference-control loop	Petzschner et al., 2017		
Phenomenological approaches to embodiment	MacLachlan, 2004; Gallagher, 2005; Thompson, 2007; Fuchs, 2008		
Bio-looping	Seligman et al., 2015; Kirmayer and Gómez-Carrillo, 2019		
Phenomena			
Abstract mental processing	Pfeifer and Bongard, 2006; Zdrazilova et al., 2018	Bullying	Mulder et al., 2020
Action perception	Buxbaum and Kalénine, 2010; Gredebäck and Falck-Ytter, 2015	Gender	Zhang et al., 2018
Aesthetic judgement	Kirsch et al., 2016; Gallese, 2017, 2019	Enriched environments	Cortes et al., 2019
Emotion contagion	Fawcett et al., 2016, 2017	Racial discrimination	Brody et al., 2016
Emotion perception	Adolphs, 2002; Vermeulen and Mermillod, 2010	Socio-economic status	Needham et al., 2015; McDade et al., 2019
Interoception	Craig, 2004, 2009b; Seth, 2013; Seth and Friston, 2016	Traumatic events	Ramo-Fernández et al., 2015; Kuan et al., 2017
Joint action	Sebanz et al., 2006; Vesper et al., 2010		
Joint attention	Moore et al., 1995; Eilan, 2005		
Language development	Rizzolatti and Arbib, 1998; Fuchs, 2016b; Inkster et al., 2016; Sidhu and Pexman, 2016		
Mental health	Herbert and Pollatos, 2012; Petzschner et al., 2017; Khalsa et al., 2018		
Motor imagery	Lotze and Halsband, 2006; Filimon et al., 2007; Munzert et al., 2009		
Social perception and judgement	IJzerman and Semin, 2010; Kang et al., 2011; Meier et al., 2012		
Fields of research			
Cognitive psychology		Anthropology	
Computational psychiatry		Epidemiology	
Human movement science		Genetic psychology	
Robotics		Social psychiatry	
Social psychology			
Sports psychology			

Environmental approaches to embodiment, on the other hand, explicitly examine the developmental outcome related to the environmental impact under study. The goal is to trace the underlying biological processes, which lead to the observed associations in longitudinal epidemiological data (Hanson and Gluckman, 2008; Rutter, 2016; see also references in **Table 1**). This "archeology" (Hertzman, 2012, p. 17163) digs into different biological layers to ultimately identify differences at the level of DNA methylation or protein activity and gene expression. Although environmental approaches to embodiment assume that the incorporation or embedding of experience potentially takes place at multiple time-points, they often register only single events (preferably in early childhood) and their impact on a single biological level (e.g., the genetic and epigenetic level: Godfrey et al., 2007; Caspi et al., 2010). Only rarely, dynamic cross-level transformations of incorporated experiences are studied. This is mainly due to method- and data-related constraints. It implies, however, that we register only main tendencies and might miss most of the environmental impact and biologically embedding of dynamic experiences over the lifespan. In most cases, the "digging process" is limited to the final time-point and one biological condensate of interest.

In this way, environmental approaches often imply a direct causal link between an environmental event and a behavioral pattern, differences in psychological functions, or a mental health outcome. However, there is limited evidence for cases in which an input early in life directly, exclusively, and irreversibly affects the long-term outcome. More often we must assume that the biological foundation undergoes several dynamic developmental processes throughout an individual's life. Also, the mechanisms underlying acute activation of embodied experiences might differ from those grounding the long-term developmental pathways which channel the activation outcome. An experience may be embodied in a way that shapes a developmental pathway, which is then channeling but not determining the acute activity patterns, such as determining hormonal setpoints in the stress response system. This is critical, as any identified mediators and intermediate developmental stages of embodiment processes open up targets for interventions.

Table 2 summarizes developmental theories and their critical propositions for developmental embodiment research.

DEVELOPMENTAL EMBODIMENT RESEARCH: CROSS-DISCIPLINARY EXAMPLES

Practical examples of interdisciplinary embodiment research are still rare. Among these examples, only a few explicitly address embodiment processes from a developmental perspective. Here, we present a small selection of them, which shows the range of disciplines and research fields for which a developmental perspective of embodiment provides a useful platform. We selected these examples to illustrate the productivity but also some of the challenges of our proposed framework. Because of the many-faceted conceptualization of embodiment in the life sciences, the following examples can only be spotlights, highlighting different levels and areas of embodiment research, where, e.g., a developmental perspective is already employed, but needs refinement and more systematic standards across timepoints and experimental systems (see section Example 5: Epigenetic Mechanisms as Biomarkers for the Impact of Early Life Stress on Mental Health), or where such a perspective would help integrate data (see sections Example 1: Age-Related Cognitive Decline Impacts Motor Control and Example 4: The Developmental Impact of Limited Interoceptive Perception in Autism Spectrum Disorders) or provide additional criteria for competing theoretical explanations (see section Example 3: The Role of Sensorimotor Systems in Abstract Concept Representation and Example 7: Modeling Motor and Cognitive Development With Robots). Also, the examples described in the following demonstrate that the integration of timescales and levels needs to be case specific for each embodiment phenomenon, since, depending on the methods and data available, studying cross-level effects and indicators of long-term changes are quite different across disciplines and research topics.

Example 1: Age-Related Cognitive Decline Impacts Motor Control

One first example, for how current interdisciplinary embodiment research profits from an explicit developmental perspective, is motor decision making. Decision making research has a long tradition in psychology. However, its relevance for understanding changes in movement coordination of everyday activities such as reaching and grasping has only recently been acknowledged: Cisek (2007), Cisek and Kalaska (2010), and Cisek and Pastor-Bernier (2014) highlighted the embodied nature of motor decision making, and its temporal dynamics during movement planning and control in a series of theoretical papers. Following this approach, Gallivan and Chapman (2014), Gallivan et al. (2018), Krüger and Hermsdörfer (2019), and Salzer and Friedman (2019) provided empirical evidence for these assumptions by showing changes in the execution of reaching movements under different conditions for motor decision making. It has been suggested that the perceived or expected biomechanical costs of a movement can reverse decisions to reach to particular targets (Burk et al., 2014) and can bias perceptual decision making when coupled to motor responses (Hagura et al., 2017). Thus, embodiment research, spanning the levels of neural, sensory, and motor activity, as well as complex psychological function and behavior, has advanced the cross-disciplinary understanding of decision making processes. Still, what is largely missing at present is the integration of empirical evidence on lifespan developmental changes of cognitive, perceptual and motor processes, stemming from the different research disciplines, into (motor) decision making theories: i.e., how age-related changes in cognitive and perceptual decision making, due to age-related changes in cognitive functioning and underlying neural networks (Mata et al., 2007; Eppinger et al., 2011; Kurnianingsih et al., 2015), relate to age-related changes in movement coordination and motor function (Verrel et al., 2012; Krüger et al., 2013), and vice versa. A developmental perspective on embodiment would allow for this integration by highlighting the dynamic and mutual interrelationship between motor and cognitive functioning across the lifespan, potentially also providing hints for the origins of the increasing inter-individual variability in cognitive and motor functioning with increasing age. In addition, it opens new avenues for research in the context of neurorehabilitation, since it underlines the need for multi-professional interventions to alleviate motor and cognitive impairments after e.g., stroke.

Example 2: Motor Expertise Changes Perception and Cognition

In a different context, the interaction between motor skills, perception and cognition, and their neural basis is already studied from a developmental perspective, but on a much shorter timescale than lifespan development: In research on motor expertise, a developmental perspective has been adopted to measure how the adult brain changes during motor skill learning and physical training (Wenger et al., 2017). This approach of observing the dynamics and patterns of neuroplasticity during motor learning might contribute to explaining embodiment phenomena found in this context. Several studies convincingly showed that motor expertise changes perception and cognition. Movements which had been extensively trained were more readily recognized in subsequent visual discrimination tasks

TABLE 2 | Lifespan developmental theories and their critical propositions and implications for developmental embodiment research.

	Critical propositions	Implications	References
Developmental systems theory			Oyama, 2000; Bjorklund, 2003; Lickliter and Honeycutt, 2003; Overton and Lerner, 2012; Griffiths and Tabery, 2013
	Developmental cascades: • Capturing cumulative effects within a developmental pathway brought by the multiple interactions occurring in developing systems after an environmental input or another developmental event • Spreading across levels, among domains at the same level, or even across developing systems and generations	• Identify developmental cascades with cross-levels effects underlying embodiment phenomena	Masten and Cicchetti, 2010
	Procedures: • Referring to biological forms, structures, and patterns, but also chemical gradients etc. channeling the developmental process	• Embodiment phenomena result from an inherent parallelism of developmental changes and stability	Overton, 1991
Gene-environment interaction models			Hunter, 2005; Caspi et al., 2010; Esposito et al., 2018
	Differential susceptibility hypothesis: • Genomic information might not always directly affect the final phenotype but mediate the way, environmental influences and conditions get integrated during the course of development	• Genotype functions as embodied resource potentially shaping the degree to which environmental influences get incorporated during the life course	Belsky and Pluess, 2009; Pluess and Belsky, 2010
Lifespan developmental psychology			Baltes, 1987; Baltes et al., 2006; Li, 2006
	Co-occurrence of gain and loss: • Functional domains show different developmental trajectories as well as different ranges of changeability or plasticity	• Identify the mechanisms underlying processes of gain and loss at different biological level	Brandtstädter and Greve, 1994; Baltes et al., 1999; Staudinger and Baltes, 2001
	Sociocultural-historical context and timeframe: • Ontogenetic development as lifelong process of dynamic and selective adaptation based on the interaction of biological, cultural, and context factors	• Identify socio-cultural variation in developmental pathways with potential impact on incorporation and expression of embodied experiences	Baltes, 1987
Lifespan perspective on motor development			Thelen et al., 1987; Kamm et al., 1990; Schmuckler, 1993; von Hofsten, 2004; Haywood and Getchell, 2020
	Rate limiters: • In the interaction of individual, environmental, and task constraints during motor development, individual constraints at each system level can either support or hinder the development of new or the maintenance of existing motor skill	• Cross-level effects in the process of evolution and involution of motor capabilities underlying embodiment phenomena	Newell, 1986
	Interrelationship of developmental timescales: • Embeddedness of motor learning within the process of motor development and mutual responsiveness of both	• Consider different developmental timescales of processes underlying embodiment phenomena	Adolph, 2019

A variety of developmental theories, models, and frameworks, targeting different system levels, provide conceptual and methodological foundations for an interdisciplinary framework, which integrates agency and environmental approaches to embodiment. The table provides an overview of these developmental theories, with their critical propositions and related implications for developmental embodiment research.

(Casile and Giese, 2006; Aglioti et al., 2008). Importantly, these perceptual improvements cannot be explained by visual experience alone, but suggest motor learning-induced plasticity in the sensorimotor system to affect perception and cognition as well. This is in line with several theoretical assumptions. One of them is the common coding account which considers overlapping representations of action and perception (Prinz, 1997). It also fits with the notion that neural networks for motor control have evolved to contribute to both motor actions and cognition (Ptak et al., 2017), which, again, is in line with a dynamic systems approach to cognitive development (Thelen, 2000) and with the predictive coding framework (Kilner et al., 2007). From this perspective, it is a pressing research question whether and how neuroplasticity in the sensorimotor system accounts for the development of special cognitive and perceptual skills in movement experts.

Example 3: The Role of Sensorimotor Systems in Abstract Concept Representation

A developmental approach could also provide valuable new insights into the mechanisms underlying the representation of abstract concepts. In particular, by studying children's acquisition of abstract vocabulary we can test claims about the role of sensorimotor systems in knowledge representation (for a review see Pexman, 2019). Currently, at one end of the spectrum, amodal theories posit that knowledge is represented symbolically, which means that concepts are distinct from the ways we experience them (e.g., Quillian, 1969; Pylyshyn, 1985). At the other end of the spectrum, strongly embodied theories posit that knowledge is grounded in sensory, motor, and emotion systems (e.g., Glenberg and Gallese, 2012; Glenberg, 2015). Between these poles lie multimodal or hybrid theories, which posit that knowledge is represented in many ways (e.g., language, emotion, introspective, and sensorimotor) and that different kinds of information are important for different types of concepts (e.g., Barsalou et al., 2008; Borghi et al., 2019). These theories have been tested extensively in the context of research on adult concepts and language processing, with much recent support for multimodal theories (for a review see Zwaan, 2014). The underlying predictions about the acquisition of word meanings during language development in children have only begun to be tested (Wellsby and Pexman, 2014), with a handful of recent studies testing the validity and area of application of two competing theoretical proposals, the emotion bootstrapping proposal (Ponari et al., 2017, 2020; Lund et al., 2019) and the language competence proposal, suggesting that future studies should more carefully consider children's acquisition of different types of abstract words (Lund et al., 2019). These recent studies provided some initial insights, but their cross-sectional designs and methods offer limited inferences about children's representations of abstract concepts. Studies have not yet systematically explored the predictors and outcomes of abstract vocabulary acquisition.

Example 4: The Developmental Impact of Limited Interoceptive Perception in Autism Spectrum Disorders

Selfhood and emotions have long been understood to be grounded in representations of the physiological state of the body (James, 1994; Damasio, 1999; Critchley et al., 2004; Craig, 2009b; Seth, 2013). More recently, research into interoception has demonstrated the extensive significance of our inner bodily signaling systems for decision making, time perception, emotion processing, and behavior in general (for review, see, e.g., Herbert and Pollatos, 2012; Seth, 2013). Consequently, for disorders that involve disturbances of self-representations (e.g., psychosis), emotional processing (e.g., alexithymia, anxiety and mood disorders), or with strong somatic components (e.g., depression and eating disorders), a primary dysfunction in the perception and regulation of body states has been considered (Paulus and Stein, 2010; Herbert and Pollatos, 2012; Stephan et al., 2016; Petzschner et al., 2017; Khalsa et al., 2018). An example are autism spectrum disorders (ASD), a spectrum of neurodevelopmental conditions characterized by lifelong difficulties in social and emotional functioning (among other impairments, Frith, 2014). ASD have been hypothesized to be related to interoceptive failure (Quattrocki and Friston, 2014). However, studies investigating interoceptive abilities in adults with ASD have yielded mixed results (Garfinkel et al., 2016; Shah et al., 2016; Gaigg et al., 2018; Palser et al., 2018). Critically, these discrepancies can potentially be resolved by adopting a developmental perspective: Quattrocki and Friston (2014) suggest that during a critical period of early childhood development, interoceptive signals need to be contextualized to support a typical development of emotional awareness and social attention. In particular, the association of interoceptive signals of warmth and satiety with an infant's caregiver serves as the basis for attachment behavior and endogenous social attention. The authors theorize that a difficulty in interpreting one's own bodily signals early on, potentially caused by abnormal regulation of the oxytocin system in ASD, prevents such associative learning between interoceptive and exteroceptive (social) cues, and leads to impairments of emotional awareness and social interaction later in life. Consistent with these ideas, recent studies support a diminished interoceptive accuracy in children with ASD (Nicholson et al., 2019), and specific impairments in the integration of interoceptive and exteroceptive information (Noel et al., 2018). However, data on interoceptive abilities in infants are scarce (although suitable experiments have been proposed) and very little is known about how these abilities develop across the lifespan (Murphy et al., 2017).

Example 5: Epigenetic Mechanisms as Biomarkers for the Impact of Early Life Stress on Mental Health

One example for the potential but also the difficulties to identify links between different levels of embodiment when following an environmental approach is research investigating epigenetic mechanisms underlying long-term mental health effects of early life stress. Data from several longitudinal studies, clinical samples, as well as animal research support the link between early life stress and mental health (see the review by Provençal and Binder, 2014). Although some assume that the effects of early life stress only impact the individual after multiple stressful experiences (Binder et al., 2008; Danese et al., 2011; Zannas et al., 2015), there is consensus among researchers that early life stress gets somehow biologically embedded or embodied during critical periods in a way that mediates later effects. A growing body of research has identified stressor specific effects and effects of different stressor intensities (Bock et al., 2015; Lux, 2018; Aristizabal et al., 2019), as well as several factors of resilience or reversibility (Harris et al., 2016; Serpeloni et al., 2019; Hartmann and Schmidt, 2020, Francis et al., 2002). The main challenge for the research field is to determine the causal pathway that integrates effects of different embodiment levels (from molecular to behavioral and cognitive) at several critical time points across the lifespan, and especially in early life periods.

Here, one line of research focuses on epigenetic modifications as relatively stable intermediate level, coordinating genetic constitution, and environmental signals, as indicated by animal studies (Weaver et al., 2004; Murgatroyd et al., 2009; Franklin et al., 2010). Although epigenetic modifications following early life stress are reported repeatedly (for a review see Aristizabal et al., 2019; with focus on human studies Vaiserman, 2015), mechanistic links between these and other levels of embodiment including the stress hormone system and stress and emotion regulating neural networks are still not identified (Aristizabal et al., 2019). Instead, contradictory findings complicate the picture. To make sense of the current findings, the field works at developing integrative models spanning different time-points of embodiment and highlighting critical periods, during which exposure to adverse environments and stress impacts developmental pathways much stronger than during other periods over the lifespan (Lupien et al., 2009; Bock et al., 2015; Non et al., 2016; Non, 2021). In addition, more research is needed to distinguish between long-term epigenetic modifications observed following early life stress and those related to acute stress exposure later in life, to determine the importance of developmental timing and cumulative effects. Trans- and inter-generational effects in mammals and humans are implicated but very challenging methodologically to determine, and thus still under controversial debate (Horsthemke, 2018; Lacal and Ventura, 2018; Perez and Lehner, 2019).

Example 6: Identifying Sensitive Periods for the Incorporation of Embodied Experiences

An example of research that could address the question of critical periods using a developmental framework are experiments that can establish causation and go beyond traditional observational studies. For example, Provençal et al. (2019) tested epigenomic effects of exposing fetal-derived neurons *in vitro* to stress hormones (glucocorticoids) across different time periods of exposure, and even how they prime future gene expression responses to stress. While experiments like these are divorced from interactive effects in the body, they can be a first step toward establishing if and when critical periods for stress exposure may alter the epigenome in the relevant tissue of interest. These experiments, of course, test only short-term early life embodiment and would benefit further by integrating findings with longitudinal human studies to see if the same epigenetic effects last throughout the life-course across accessible tissues and contribute to long-term mental health effects. For this, the research field would clearly profit from knowledge about the developmental dynamics of embodiment processes. Although epigenetic mechanisms are still the primary focus, more complex cross-level effects of stabilization and mediation, especially between epigenetic modifications, the stress hormone system, and the formation of neural networks have been identified as promising targets for this line of research (Lux, 2018; Aristizabal et al., 2019; Fogelman and Canli, 2019, Hartmann and Schmidt, 2020).

Example 7: Modeling Motor and Cognitive Development With Robots

In the field of human robotics, the turn to embodied cognition theories initially went against the information processing paradigm of artificial intelligence (AI) (see Hoffmann and Pfeifer, 2018). Until then, AI units constructed according to the information processing paradigm showed tremendous success in pattern recognition and human-like learning behavior, but they were strongly limited by the available processing capacity. The turn to embodied cognition theories within robotics was supported by the production of simple robots imitating the anatomy of living organisms and showing stable and sophisticated motor and sensory behavior without the need of complex information processing systems. One of the most striking examples is the passive dynamic walker, inspired by the anatomy of human legs, which is able to walk stably and smoothly on a plain surface due to its mechanical properties and without complex processing of movement control (McGeer, 1990; Collins et al., 2005). In a similar way, Brooks developed robots with simple parallel sensory processing units, partially hierarchically clustered, which navigate successfully within their environment without the need of complex representation (Brooks, 1991). However, these example robots, as impressive as they are, are restricted to on-time processing of the 'here and now' and not able to learn from previous experiences. A developmental perspective on embodiment, combining the embodied cognition approach with machine learning and similar algorithm-based self-controlled processing shows promising potential for overcoming some of the boundaries inherent to each approach (Bongard et al., 2006; Sloman, 2009; Hoffman, 2012; Hoffmann and Pfeifer, 2018), with first computer models (Hoffman, 2012) and prototypes being developed. These robots use mechanically inbuilt embodied information to guide motor control and sensory input to reduce processing capacities necessary for interactions with the environment, which are then free for complex, i.e., capacity demanding cognitive processes, e.g., learning.

In addition, human robotics research based on a developmental embodiment perspective also provides a platform and model for the study of human cognition and motor development by allowing to control and observe the functional elements as well as the developmental processes to a degree which is not possible in living organisms (Pfeifer and Bongard, 2006; Hoffmann and Pfeifer, 2018). For example, based on a computational approach to developmental systems neuroscience, Schöner et al. (2018) simulated a simple neural dynamic model of movement generation, serving as platform for discussing infants' developmental challenges as they learn to reach for objects. Also, based on this model, they were able to construct a neural inspired robot imitating the neural processes underlying the reaching behavior (Tekülve et al., 2019). Although such modeling approaches are limited to engineering and computing capacities, they provide a potent tool to test hypotheses between different levels of embodiment, especially between the neural network level and the level of sensorimotor processing and motor actions.

TOWARD AN INTEGRATIVE FRAMEWORK FOR DEVELOPMENTAL EMBODIMENT RESEARCH

As the previous examples show, developmental embodiment research focuses on cross-level effects underlying developmental processes, and a lifespan perspective to overcome restrictions of previously used approaches within their disciplines. An interdisciplinary framework acknowledging this research approach has the power to provide a matrix and platform for specific empirical studies or experiments on embodiment processes and phenomena, executed based on discipline specific standards and methods. Such a framework, as we propose in the following, maps out connections between levels of embodiment, with the goal to identify and address white spots across the map which, when filled, further complete the picture of a specific embodiment phenomenon. In this section, we will first introduce the main pillars of our framework and then outline important steps to bridge different timescales and levels of embodiment in cross-disciplinary embodiment research.

Environmental and agency approaches represent complementary perspectives. As **Figure 1** illustrates, environmental and agency approaches to embodiment represent complementary perspectives in this endeavor: While environmental approaches focus on the process of *incorporation* of experiences over the lifespan (green arrow), agency approaches focus on the process of *expression* of embodied capacity within a specific behavior, emotional state or functional ability, simultaneously expressing and, through the action etc., *shaping* bodily preconditions (orange and yellow arrow). Both complementary, but analytically distinct approaches are interconnected by developmental processes along the individual's developmental timeline (gray-colored circular arrow).

Multi-level approach. In addition, **Figure 1** illustrates the different physiological and functional levels potentially involved in the processes of incorporation, shaping and expression of embodied experiences. At the moment, these levels are often studied separately in different disciplines and by different theoretical schools, depending on their respective concept of embodiment. An explicit developmental perspective, relying on critical propositions of developmental theories, shifts the focus on the developmental processes interconnecting the mechanisms underlying a specific embodiment phenomenon at the different levels.

For example, from a developmental embodiment perspective, epigenetic modifications as well as the underlying genotype could be understood as developmental resources. These resources shape the way and degree to which environmental influences are incorporated during the life course and impact developmental outcomes, cumulating, for example, in disease vulnerability or resilience. These then represent some of the underlying bodily preconditions, for example, in a situation of acute mental distress, potentially shaping the symptomatic re-/action to a stressful situation. Pluess and Belsky (2010) discussed these observations as *differential susceptibility* to environmental signals (see **Table 2**) and *environmental sensitivity* (Pluess, 2015), Weaver et al. (2004) framed it as *epigenetic programming*. The impact of molecular changes at the epigenetic level on the adult phenotype, including disease symptoms and responsiveness to therapy, is a pressing research question. Specifically, at the genetic and epigenetic level (greenish level in **Figure 1**), environmental epigenetics (Weaver et al., 2004; Zhang and Meaney, 2009; Bollati and Baccarelli, 2010) and studies of gene-environment interactions (Caspi et al., 2003, 2010; Risch et al., 2009; Culverhouse et al., 2018) analyze molecular long-term (ontogenetic) effects of embodied experiences. In addition to one-time severe impacts, such as traumatic events or toxin exposure, also multidimensional and enduring environmental signals are studied, such as enriched environments (Zhang et al., 2018), bullying (Mulder et al., 2020), racial discrimination (Brody et al., 2016), socio-economic status (Needham et al., 2015; McDade et al., 2019), social deprivation (Non et al., 2016), and gender experiences (Cortes et al., 2019). For these fields, our framework would provide the currently missing cross-disciplinary matrix to integrate the different time-points and levels under study.

Accounting for change and stability. Further, from a developmental embodiment perspective, we conceptualize embodiment phenomena as resulting from a balance of developmental change and stability, which depend on the presence, strength, and timing of the environmental signal. Coming from Developmental Systems Theory, which emphasizes that the developmental system consists of dynamic feedback loops, Overton (1991) introduced the term *procedures* to characterize temporarily stabilized parts of the developmental systems present in embodiment phenomena (see also **Table 2**). Bones, grown structures and patterns of tissue, muscle constitutions and setpoints within metabolic or hormonal feedback loops, neural pathways and networks, epigenetic modifications but also automized behavioral patterns potentially function as established and stabilized procedures sculpting developmental pathways. Although procedures continuously need to be maintained within the developing system, we can classify them as embodied when the energetic costs to transform a procedure outweigh those to stabilize it, keeping in mind that the balance between energetic costs for stabilizing a procedure and transforming it might change during the course of the lifespan.

For example, the hormonal feedback loops underlying the stress response are established early in development. During this critical developmental period, set points of up- and downregulation of the stress response in presence of an acute stressor are established depending on the individual metabolic conditions and stress experiences during this period. These are

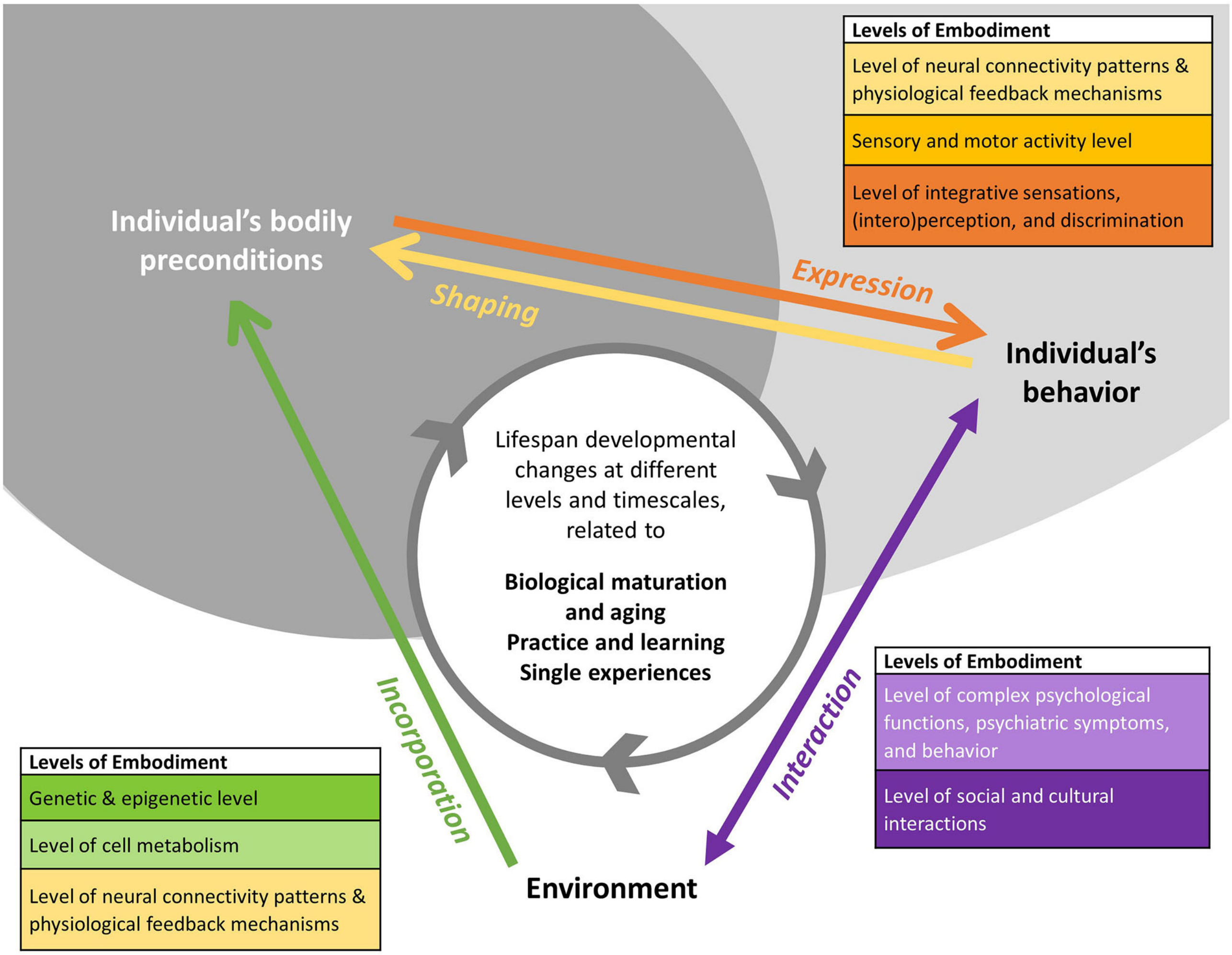

FIGURE 1 | Developmental perspective on embodiment. The figure illustrates how different conceptualizations of embodiment relate to each other from a developmental perspective. Arrows represent the different embodiment processes with the colors indicating the physiological and functional levels at which they are analyzed. The direction of the arrows indicates the perspective on the person-environment relationship. While *environmental approaches* focus on the process of incorporation of experiences over the lifespan (green arrow), *agency approaches* focus on the process of mobilization of embodied experiences and knowledge (purple arrow) within a specific behavior, emotional state or functional ability, simultaneously expressing and, through the action etc., shaping bodily preconditions (orange and yellow arrow). The developmental perspective emphasizes that both types of processes change the person-environment relationship. Lifespan changes of bodily preconditions, occurring at different timescales, result in lifespan developmental changes of embodiment phenomena and processes (gray colored circular arrow).

then stabilized, however, the stabilization might be challenged by following life experiences, such as traumatic events, hormonal imbalances during adolescence, pregnancy, chronic stress, or aging, which all might lead to changes of the original set-point. The exact mechanisms of stabilization and change of these set-points are still only partially known, yet, it is assumed that they contribute to stress-related mental health impacts.

Another example would be establishment of neural pathways underlying automatized word recognition in reading. The ability to learn how to read depends on age-dependent neural and cognitive development with only some degree of inter-individual variability indicating dependence on other bodily embedded developmental processes. Once the basic ability to learn how to read is developed, instructions and practice are needed until the stage of automized word recognition is reached. The neural mechanisms, such as synaptic sensitization and neural pathway stabilization, underlying this automatization process are likely similar to (and may even rely on) processes of automatization of other motor and sensory activities, yet, again, they are still partially known. Their further elucidation would contribute to our knowledge on the mechanisms underlying various variants of dyslexia as well as possible impacts of strokes and subsequent rehabilitation therapy.

Developmental embodiment research would address these mechanisms with a multi-level cross-disciplinary approach and lifespan perspective. It would also address that the pathways of embodiment are then potentially two-fold, as can be traced in **Figure 1**, via a more passive incorporation (green arrow) or via the expression-shaping cycle (yellow and orange arrows) mediated by the individual's interaction with the environment (purple arrow). As both are depending on each other, with acute activation necessary for change and maintenance on the one side and incorporation setting some of the preconditions for the activation process on the other side, overcoming the current practical divide in embodiment research between environmental approaches and agency approaches is crucial to further advance our understanding of these processes. Interconnecting them via a developmental perspective would allow to assess criteria and thresholds for change and stability at a specific level (of, for example, genetic and epigenetic activity, cell metabolism incl. hormonal activity, neural network activity, sensory, and motor activity) within different developmental periods across the lifespan.

Cross-level effects cumulating in developmental cascades. An explicit developmental perspective on embodiment, building upon critical propositions of developmental theories, also highlights the cross-level dependencies and effects of embodiment processes and phenomena. According to the life span perspective on motor development (see, for example, Haywood and Getchell, 2020) skilled motor behavior follows from a self-organization process of multiple system levels within an individuum, e.g., muscular, skeletal, neural, cognitive, etc., referred to as "individual constraints" (Newell, 1986). Based on this assumption, it follows that, for developmental motor behavioral changes to occur, all individual constraints have to be developed to a required level. Here, the proposition that individual constraints can act as *rate limiters*, i.e., either restricting or facilitating the development or decline of motor skills, implies cross-level dependencies of development (see also **Table 2**). Masten and Cicchetti (2010) discuss such cross-level effects under the term *developmental cascades* (see **Table 2**). Developmental cascades capture cumulative effects within a developmental pathway brought by the multiple interactions occurring in developing systems after an environmental input or another developmental event. The key characteristic of such a cascade is that the effect spreads across levels, among domains at the same level, or even across developing systems and generations (Masten and Cicchetti, 2010, p. 492). From the perspective of developmental embodiment research, it would then be the goal to identify developmental cascades with cross-levels effects underlying embodiment phenomena. This also stipulates identification of levels involved and affected within a specific embodiment phenomenon, identification of transmission hubs between these levels as well as identification of time-points of transmission. These differ for the particular phenomenon under study, e.g., for the biological embedding of early adversity and its long-term impact on mental health, the way motor experiences ground the development of cognition and emotion processing, and how imagination techniques improve motor rehabilitation outcomes after a stroke.

Identification of transmission hubs. Trying to identify developmental cascades when taking the systemic and dynamic character of biological processes seriously, as from a developmental systems perspective, would require to account for all levels of the system at every time-point during development. However, such a comprehensive approach is not feasible in concrete empirical studies, even with cross-disciplinary collaborations addressing different levels, timescales, and data modalities. Therefore, we propose to focus on the identification of transmission hubs between levels of embodiment. Transmission hubs constitute the molecular, physiological, cognitive, etc. structures which participate in the transmission of signals related to a particular embodied experience across levels, such as, e.g., neural networks underlying motor execution that are also involved in imagination and cognitive processing, neural and hormonal correlates of interoception in emotion processing and related disorders (see section Developmental Embodiment Research: Cross-Disciplinary Examples, Example 4), molecular feedback loops underlying the regulation of synaptic plasticity, neurotransmitter activity, and the stress response, as well as processing of biomedical knowledge influencing self-perception, symptomatic experiences, and mental health. These transmission hubs are characterized by their critical role to enable or block transmission of developmental changes between levels, thereby stipulating and canalizing embodiment processes. Importantly, with respect to the developmental perspective, transmission hubs are not fixed across the lifespan, but change due to developmental processes, e.g., in the degree of plasticity, the involved biological, and functional levels of transmission, the signal intensity needed to induce transmission. They are also likely involved in the constitution of critical and sensitive periods but not limited to them.

Accounting for gain and loss. From research in the perspective of lifespan developmental psychology, we draw on the notion that gain and loss always occur together in ontogenetic development (Baltes, 1987) for our integrative framework for developmental embodiment research (see also **Table 2**). Thus, in addition to analyzing growth and maintenance as well as recovery and resilience, studying the regulation of loss is equally important. While lifespan developmental psychology focuses on the developmental consequences of this selective channeling process, developmental embodiment research additionally aims at identifying the mechanisms underlying these processes at different biological levels.

Functional domains differ in their developmental trajectories. Also in reference to research in the perspective of lifespan developmental psychology, we account for the notion that different functional domains have different developmental trajectories across the lifespan, which also differ in their range of changeability or plasticity and even between individuals with comparable functional outcome (Brandtstädter and Greve, 1994; Baltes et al., 1999; Staudinger and Baltes, 2001). As a methodological consequence, person-centered (holistic) and function-centered approaches need to be combined to study these developmental trajectories (Baltes et al., 1977; Baltes, 1987). Although a function-centered approach will probably be used most in developmental embodiment research, a person-centered approach might become more relevant when the field expands into translational research and when focusing on inter-individual differences in the expression of embodiment phenomena.

Accounting for sociocultural-historical changes. Finally, a developmental embodiment perspective reinforces the necessity to account for sociocultural-historical changes and their impact on the bodily preconditions of psychological functions. This includes the effects of socio-cultural contexts (family, school, work, etc.), historical changes of educational and professional systems, cultural norms, (religious and other) traditions, as well as historic events, such as war periods and collective traumatic events. Some examples following an environmental approach to embodiment are efforts to identify epigenetic mechanisms underlying the long-term impact of traumatic events such as the attacks of 9/11 (Kuan et al., 2017) or war crimes (Ramo-Fernández et al., 2015). Another example in this perspective are studies on changing neural networks and cognitive performance in children after entering school (Brod et al., 2017). Examples following an agency approach to embodiment are analyses of bio-looping effects of cultural knowledge and resources including scientific concepts and how they influence the active construction of self-perception patterns and identity, emotion regulation, and health and body related behavior (Seligman et al., 2015; Kirmayer and Gómez-Carrillo, 2019).

Thus, for developmental embodiment research, considering lifespan dynamics of embodiment does not only entail the consideration of different timescales of development, but also the consideration of different processes, which contribute to these developmental changes and the different timescales at which these processes act. Reconstructing the developmental cascade therefore requires integrating data generated with different experimental settings and study designs, at different time-points, at different levels, and across the involved disciplines.

Bridging Timescales of Embodiment

With our framework for developmental embodiment research, we explicitly aim at bridging the different timescales of embodiment focused on either by agency or environmental approaches (see **Figure 1**).

First, we emphasize studying developmental processes related to embodiment phenomena along different timescales, foremost across the whole lifespan. Due to the underexplored lifespan perspective, buffering effects and functional changes during development are often underestimated, as shown, for example in research on the biological correlates of resilience (Feder et al., 2009) and longitudinal studies of stress buffering effects of social support and mental function in old age (Toyama and Fuller, 2020). To identify these, the study of functional gains should be complemented with the study of mechanisms of maintenance and of the regulation of loss, as well as with the search for alternative developmental pathways in studies using inter-individual comparisons. However, shorter timeframes of developmental dynamics also have to be considered as periods in which such alternative developmental pathways are initiated. When considering development as a result of interacting constraints at different system levels within the individual, and between the individual and the environment, single events, as, for example, traumatic experiences or learning processes may lead to immediate changes of developmental pathways, with lifelong consequences for related embodiment phenomena. Thus, depending on the phenomena under study, also shorter timeframes of analysis, e.g., for specific learning processes, or a repeated analysis of shorter timeframes spread out across the whole lifespan, as often used in longitudinal studies, should be considered for being able to identify buffering effects und functional changes across the lifespan.

Second, despite a focus on the whole lifespan, we also need to continue identifying sensitive periods during which experiences are more likely to be embedded. For this, we need to consider that sensitive periods differ across different neural and other physiological systems contributing to motor, cognitive, and brain development. Moreover, the study of sensitive periods, such as the perinatal phase, early childhood, and adolescence, needs to be complemented by the study of subsequent stabilization periods, and phases of recession and degeneration in later life. Only when the embodied experience, as acquired through interaction with the environment, is preserved, can it be relied on at a later time-point and can thus have a developmental impact. These stabilization processes might provide promising targets for intervention, especially with regard to later phases of accelerated decline in functioning at multiple behavioral and physiological levels.

Third, for every behavioral outcome, symptom, or function studied in terms of embodiment, commonalities but also differences between the biological processes contributing to the incorporation of experiences and those used for expressing the embodied experiences during action need to be taken into account. This is of particular practical relevance for interventions, which may differ significantly in their structure and outcome depending on whether they target the first or the latter. For example, in the context of mental health, an intervention might aim at increasing resilience (to prevent incorporation of negative experiences), or it might aim at increasing behavioral flexibility and at re-learning after a negative environmental impact (such as cognitive-behavioral interventions), or at interfering neurochemically with the circuit that implements the embodied processes (as pharmacological interventions do).

Fourth, depending on the system level, an evolutionary timeframe needs to be considered. Identification of phylogenetic evolved plasticity and environmental sensitivity parameters for specific target systems and tissue will inform clinical and intervention studies. However, it is important to not confuse the phylogenetic timeframe, which addresses species development at the population level in a co-developing organism-environment context, and the ontogenetic timeframe within the lifespan of an organism. Developmental dynamics of different physiological systems or neural networks will vary between individuals. Identification and description of species-specific developmental periods needs to account for this variability.

Fifth, across these different timescales of phylogenetic developed sensitive periods, their socially and culturally shaped realization during ontogenetic development, and such single short-term experiences with long-lasting effects, we suggest focusing on the transmission hubs underlying developmental processes, which connect processes and functions at different levels with each other and provide transition points within the developmental pathways. One example would be the study of traumatic stress during sensitive periods of brain development contrasted with traumatic stress experienced before or after such a sensitive period. The transmission hubs of interest here would be those hormonal, neural, and molecular feedback loops whose interaction constitute sensitive periods thereby opening up the involved systems for the embodiment of the environmental signal.

Bridging Levels of Embodiment

In addition to accounting for different timescales that underlie the processes of incorporating and expressing embodied experiences, we propose that a developmental perspective allows for connecting different biological and functional levels of embodiment. For that, the involved levels of embodiment have to be clearly differentiated to carve out conceptual and methodological gaps that need to be bridged when studying a specific embodiment phenomenon. Identification of levels is a precondition for cross-disciplinary data integration.

There are multiple ways to differentiate levels of embodiment. For the aim of our proposal—connecting different approaches of embodiment research from a developmental perspective—we differentiate between levels along the methods used to assess, observe, induce, and evaluate changes of embodiment. This is a first step in the process of integrating data from different research fields and approaches with each other, despite the conceptual variability in embodiment definitions.

We propose to differentiate between at least seven levels of embodiment (see **Table 3**): The genetic and epigenetic activity level (1), the level of cell metabolisms (including proteomics analyses) and single neuronal activity (2), the level of neural connectivity patterns and physiological feedback mechanisms (e.g., hormonal, metabolism related) (3), the sensory and motor activity level (4), the level of integrative sensations, (intero)perception, and discrimination (5), the level of complex psychological functions, psychiatric symptoms, and behavior (6), and the level of social and cultural interactions (7). The number of levels and their distinction are not exclusive. We explicitly encourage understanding them as to be open to adaptations depending on their worth for the respective empirical study and the development of new methods.

We further propose to understand these levels as analytical tools rather than empirical entities, with the purpose to identify key processes, which coordinate and translate different biological mechanisms underlying embodiment as well as psycho-social and cultural interactions related to them. The method-based differentiation of these analytical levels also enables to visualize where data acquisition at different levels may be easily combined or exclude each other (for neuroscience/fMRI see Soares et al., 2016; for genomics/proteomics see Tyers and Mann, 2003; Manzoni et al., 2016; Vitrinel et al., 2019). Also, methods which describe embodiment and embodied experiences from different epistemological standpoints that do not map easily onto each other, such as cultural analysis, introspection, and the detection of neural activity or gene expression patterns, can be made explicit in this framework (for an example on embodied memory and social skills see Fuchs, 2016a). This supports the planning process of collaborative research projects spanning across levels.

The variety of methods used to differentiate between levels of embodiment may seem overwhelming to approach from the perspective of single research groups. Moreover, technical restrictions in data acquisition and epistemological gaps between data modalities (e.g., between subjective experience data and neurophysiological data) mean there will always remain blank spaces in the picture. However, we believe that the differentiation between levels provides a clear basis for trans-level collaboration between two or more research groups and even for larger research consortia. In any case, it helps to identify the blank spaces for specific cases of embodiment phenomena. Furthermore, it allows to spot potential transmission hubs between levels of investigation. These transmission hubs are important targets to understand the process of translating incorporation into expression of embodied experiences across the lifespan. Ultimately, they also constitute promising points of intervention.

Bridging different levels of explanations (and data modalities) is a challenge that is inherent to many fields in the life sciences. A popular tool for achieving such bridges is computational modeling. Formal models of processes at different levels and their interactions allow for an *in-silico* testing of how changes at one level translate into changes at another level. One recent example is the nascent field of computational psychiatry (Huys et al., 2016; Redish and Gordon, 2016), which acknowledges the multi-leveled nature of psychiatric diseases—ranging from the genetic and molecular level, neural circuits, cognition and behavior to the social and even cultural level—and attempts to bridge these levels of analysis using mathematical tools. The even more recent subfield of computational psychosomatics explicitly considers the role of body perception (interoception) and regulation for the understanding and treatment of mental diseases (Petzschner et al., 2017, 2021). Modeling homeostatic setpoints and their interactions with cognition provides a new framework for understanding the interconnectedness of bodily and mental well-being that becomes obvious in the symptom profiles of all psychiatric and psychosomatic diseases. More generally, these approaches hold great potential for studying embodiment phenomena across different levels.

Clarifying Disciplinary Boundaries and Discipline Specific Criteria in Conceptualizing Embodiment and Embodied Experiences

One of the foremost practical challenges for integrative embodiment research, as suggested in the previous section, is that for each scientific discipline, there are different criteria for when an experience counts as embodied according to the different detection methods and data modalities. In addition, these criteria are sometimes ambivalent and need to be the subjects of further conceptual debates. Consequently, these discipline-specific criteria must be clarified for being able to relate different levels of embodiment and, consequently, embodiment approaches to each other.

At the genetic and epigenetic activity level, for example, we could ask whether detection of a functional relevant

TABLE 3 | Levels of embodiment, types of data, and biological materials or (bio-)social systems, matched with embodiment concepts by which they are addressed.

			Embodiment concepts								
Level of Embodiment	**Type of data**	**Biological material/(bio-)social system**	**Embodied cognition**	**Embodied simulation**	**Somatic marker hypothesis**	**Inference-control loop**	**Biological embedding of experiences**	**Environmental epigenetics**	**Developmental origins of health and diseases**	**Phenomenological approaches to embodiment**	**Bio-looping**
Genetic and epigenetic level	DNA sequence (genetic polymorphisms), RNA expression levels, gene × environment interactions, DNA methylation patterns, histone modifications, quantification of microRNA	DNA, mRNA, ncRNA (incl. different types of microRNA), DNA methylation, chromatin structure					🟩	🟩	🟩		🟩
Level of cell metabolism	Protein level quantification, single unit-recordings, cell anatomy measures (size, form, type, count)	Cell specific proteome, synaptic sensitivity, firing rates, cell anatomy		🟩	🟩	🟩	🟩				
Level of neural connectivity patterns and physiological feedback mechanisms	EEG, fMRI, resting state MRI, hormone levels, diverse measurements of basic metabolic functions (e.g., heart rate, breathing, blood glucose levels)	Neural network activity, hormone levels, physiological feedback cycles		🟨	🟨	🟨	🟨		🟨		🟨
Sensory and motor activity level	EEG, fMRI, behavioral observation of movement patterns, reaction time to sensory stimuli	Motor action, sensory function, neural activity in sensory and motor systems	🟨	🟨		🟨					
Level of integrative sensations, (intero)perception, and discrimination	EEG, fMRI, experimental tests of perception and basic cognitive functions (e.g., via reaction time, stimulus intensity, conflicting stimuli)	Sensory integration, basic cognitive functions, basic levels of self-awareness, pain perception				🟧				🟧	
Level of complex psychological functions, psychiatric symptoms, and behavior	Behavioral data (field observation, experimental induction), psychological and psychiatric diagnostics (test, interview), self-reports, introspection, intersubjective communication, health records	Psychosocial and physical health, first-person experiences, behavioral patterns (habits), complex cognitive functions	🟪		🟪	🟪	🟪	🟪	🟪	🟪	🟪
Level of social and cultural interactions	Qualitative interview data, discourse analysis, behavioral data (field observation), socio-economic data, epidemiological data (e.g., prevalence rates, survival rates)	Socio-cultural interactions, complex behavior, intersubjective coordination and communication	🟪			🟪	🟪	🟪	🟪	🟪	🟪

The table provides an overview about the different levels of embodiment and by which embodiment concepts they are approached. Levels of embodiment are assigned to embodiment concepts according to the type of data and the biological material or (bio-)social system addressed by the embodiment concept. Blank boxes indicate conceptual and methodological gaps between concepts within a certain level (left to right) and between levels within a concept (top to down). The addressed levels of embodiment within an embodiment concept might change due to the development and use of new methods. The matrix allows one to spot potential cross-level collaborations across embodiment concepts, but also gaps indicating the need for further research to bridge levels of interest as well as large scale methodological constraints. Each color highlights a different level of embodiment (see also ***Figure 1****).*

genetic mutation or its transcription in the target tissue, as indicated by gene expression analysis, represent the same or two different indicators of embodiment. When using epigenetic data, criteria are even more variable, including not only potential quantitative differences of functionally relevant modifications across tissue types but also different epigenetic mechanisms (DNA methylation, histone modifications, RNA interference etc.), which are functionally and hierarchically intertwined. In addition, epigenetic modifications are often evaluated as functionally relevant when they affect gene expression, although the relationship between gene expression patterns and, for example, DNA methylation is still not fully understood (Lea et al., 2018), and there may be a lag in timing before the functional effect is expressed. Thus, criteria for assessing embodiment can be too strict and not accounting for indirect as well as long-term effects of embodied experiences (Aristizabal et al., 2019), even within the research discipline.

For the level of neural activity, neural activation of motor areas either at a single neuron level or at the network level is often used as a criterion of embodiment, for example, in the detection of the fiercely debated "mirror neuron systems." Here, the activation of motor neurons during the performance as well as the perception of a motor task is used as indicator of an embodied inner simulation or immediate representation of the task (Rizzolatti et al., 1996; Rizzolatti and Craighero, 2004). From a developmental neuroscience perspective, the developmental stage of a neural network, as indicated by age-specific connectivity patterns activated in a behavioral task, also functions as criterion for the type and degree of embodied experiences (Decety and Michalska, 2020). In contrast, for the level of emotion processing and interoception, Damasio et al. (2013), first referred to a single case lesion study only showing the anatomical absence of specialized neural networks as indicator that our emotion processing abilities are grounded in bodily processes. More recently, the interaction of interoceptive and emotional states as well as with perception and cognition is investigated more systematically by testing the impact of visceral signals and their neural processing on emotional, perceptual, and cognitive functions, and vice versa (for overviews, see Critchley and Garfinkel, 2018; Azzalini et al., 2019).

For the level of complex psychological functions, psychiatric symptoms, and behavior, Needham and Libertus (2011), discussing embodiment research in the field of cognitive development, refer to the experience of acting as a main criterion for embodied experiences. Based on studies conducted by Adolph (1997, 2000), which indicate that infants do not transfer their knowledge of surface characteristics, acquired through motor experience in one type of movement (e.g., sitting), to another type of movement (e.g., crawling), Needham and Libertus (2011) conclude that the information about surface characteristics is embodied via motor experiences and not via an abstract cognitive generalization of these characteristics. Furthermore, they illustrate the asynchrony of motor and cognitive development with different results of Piaget's famous cognitive development test of object permanence (the A-not-B error task) based on the behavioral data used to measure the response (gaze vs. pointing/grasping, in 3 to 4 vs. 8 to 10-month-old infants, respectively). Needham and Libertus (2011) argue that, at this early age, the motor experience of pointing and grasping is not yet connected to the visual detection of object permanence indicating different developmental pathways. Most importantly, the different criteria at the behavioral level for different age groups (pointing/grasping vs. gaze) reveal the importance and productivity of a developmental perspective for detecting the role of embodied experiences and the degree of embodiment underlying the cognitive functions under study.

Further, for higher psychological functions such as imagination, associative thinking, and language processing, Körner et al. (2015) introduce three different mechanisms underlying embodiment effects: *direct state induction*, indicating a direct impact on how humans feel or process information without interference of any other cognitive mechanism, *model priming* referring to changes in the accessibility of concepts associated with a bodily state, and *sensorimotor simulation* indicating mechanisms which affect the ease with which congruent relative to incongruent actions are performed. Furthermore, they outline a set of conditions to test which of these mechanisms are involved in an embodiment phenomenon under study (Körner et al., 2015). For example, when the fluency of two competing tasks, which use the same sensorimotor resources, is enhanced by untraining a more fluent action (as in a right- vs. left-handed task), the underlying embodiment mechanism is based on sensorimotor simulation and not modal priming. As elucidating as this is at the level of higher psychological functions, how can we identify tasks, which use the same sensorimotor processes, in the first place (beyond right- vs. left-handed tasks)? This knowledge necessarily precedes the psychological testing conditions. Furthermore, how do we differentiate between these mechanisms when they co-occur in the studied embodiment effect? From a developmental embodiment perspective, a first step could be to trace the occurrence of these different mechanisms during ontogeny as well as to identify the potentially varying underlying neural networks.

Last, at the level of psychiatric symptoms, embodied experiences of e.g., traumatic events, or of depressive or psychotic episodes are indicated by physical symptoms and symptoms of somatization, such as pain, phantom sensations, but also hormonal imbalances and increased inflammation markers (Schnurr et al., 1998; MacLachlan, 2004; Roh et al., 2007; Abbey et al., 2011; Goldsmith et al., 2012; Blumberg and Dooley, 2017; Yuan et al., 2019).

In sum, these examples for different criteria of embodiment at different levels of investigation echo the diversity and variability in concepts of embodiment and conceptualizations of embodied experiences across scientific disciplines. Thus, it is important to clarify the criteria of embodiment for each level and discipline when conducting embodiment research. The examples also show that embodiment is often detected by studying cross-level, and, by such, cross-disciplinary effects (e.g., between motor behavior and neural activity level). Moreover, they demonstrate that the actual task is to relate the effects at each level to each other. This is especially relevant for those innovative cross-disciplinary research areas that study the processes of incorporation and expression of biological embedded experiences across system levels, e.g., in the context of cognitive development, psycho-social well-being, language acquisition and processing, preservation and rehabilitation of cognitive and motor function, and many more.

CONCLUSION

Embodiment research is at a turning point. The growing amount of data from various studies across a wide range of disciplines and theoretical schools, investigating embodiment phenomena and their role especially in mental processing and functions, highlights the need for an interdisciplinary framework of embodiment research. Innovative research areas such as movement psychology, social and developmental neuroscience, computational psychosomatics, social and behavioral epigenetics, human-centered robotics, and many more, that are facing issues of data integration across different levels of embodiment, would profit tremendously from such a framework. Especially the integration of behavioral data with data from different biological levels, each of which depend on their own developmental timescales and dynamics, is challenging for these fields. In addition, there is a growing need for a cross-disciplinary consensus on level-specific criteria of embodiment. We propose that a developmental perspective on embodiment is able to provide a framework for overcoming such pressing issues, providing analytical tools to link timescales and levels of embodiment on a case-by-case basis, uncovering the underlying developmental processes, and providing a platform to clarify and, ultimately, bridge disciplinary boundaries among the involved research fields.

The proposed framework is not intended to serve as a guideline for one comprehensive embodiment research project, but to serve as a foundation for structuring a highly interdisciplinary research field and to allow for conceptual anchor points for interdisciplinary research endeavors. Building on both environmental and agency approaches to embodiment, as well as key concepts of developmental theory, the framework motivates the question of how a specific expression of embodied experiences relates to the process of incorporation of these experiences, and vice versa, based on the underlying developmental processes. The way to reconstruct these interrelations will be specific for each embodied function, and it will have to take into account not only the rise of a function, but also its maintenance and the regulation of loss. The developmental perspective allows to, *first, connect different timescales of embodiment* based on function-specific developmental pathways. It, *second*, allows to *relate different system levels involved in embodiment processes to one another* as they develop over the lifespan, based on their physiological and functional interconnectedness. *Third*, it allows to *clarify disciplinary boundaries and their related criteria of embodiment*, which are set according to detection methods and discipline standards. The translation of different embodiment criteria between levels, e.g., the behavioral level, the level of neural activity, and the genetic and epigenetic level, heavily depends on the knowledge about the specific developmental interconnectedness between these levels and related underlying developmental pathways for each specific embodied function under study. Here in particular, further research is needed, as such translation processes also provide the basis for cross-level data integration.

First cross-disciplinary examples, as presented in section Developmental Embodiment Research: Cross-Disciplinary Examples, already point toward the productivity of such a framework, but expansion to further research disciplines is needed to fill the knowledge gaps hindering an integrative conceptualization of embodiment. For that, we propose researchers should focus on transmission hubs across two or three levels for a specific embodied function or phenomenon, aiming at identifying developmental cascades which enable cross-level effects of embodiment. These studies would depend on the knowledge about the different developmental timescales of embodied functions and sensitive periods for the incorporation of embodied experiences at the different involved levels. Our proposed framework explicitly aims at providing a matrix and platform to bridge these different developmental timescales in the study of specific embodiment phenomena and, thus, has the potential to advance cross-level, cross-disciplinary embodiment research in the short and long run.

AUTHOR CONTRIBUTIONS

The first draft of the manuscript was written by VL and MK, and all authors contributed to and commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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OPINION
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Opinion: Advancing Embodiment Research From a Developmental Point of View

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INTRODUCTION

Psychologists, neuroscientists, and philosophers are increasingly promoting the perspective that cognition is best characterized as something individuals do in practice, through their embodiment and embeddedness in the world. Contrary to the assumptions of the information processing paradigm dominant in the "cognitive revolution" of the last century, cognition is now less likely to be seen as the computational processing of representations in the brain. Rather, as (Engel et al., 2013, p. 202) have proposed, cognition is now more often seen as "skillful know-how in situated and embodied action." This action-oriented paradigm is increasingly evident in contemporary psychological science (e.g., Overton et al., 2008; Witherington and Heying, 2013; Shapiro, 2014; Marshall, 2015; Crippin and Schulkin, 2020; Dess, 2021), and there is growing acknowledgment that having the *body in action* as a central focus for theories of perception and cognition will both advance and help unify psychological science (e.g., Thelen, 2000; Overton, 2008; Glenberg et al., 2013).

In their clear and persuasive article, Lux et al. (2021) have provided a significant contribution to organizing and integrating this conceptual turn, both within and beyond psychology. Their paper provides a well-reasoned developmental framework for bridging timescales and levels of analysis within and across the various disciplines concerned with *embodiment*. Lux et al. use of a developmental framework for this integrative effort is, to my way of thinking, essential for successfully advancing the impact and application of embodiment research within and beyond psychology. The process-relational paradigm that characterizes contemporary developmental science views individuals as active agents in constructing knowledge through their embodiment and embeddedness in the physical, biological, social, and cultural environments in which they develop (Overton, 2008). From this view cognitive skills, like all of development, results from the specific activities, experiences, conditions, and resources individuals encounter and take part in as they live their lives. This developmental framework emphasizes the fundamental relations among body, brain, and world and recognizes that perceptual, motor, emotional, and cognitive functioning are inherently co-dependent. This deeply situated perspective is a far cry from the computational paradigm of cognitive science that held that cognitive functions are wholly realized by information processing mechanisms inside the brain.

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TAKING A DEVELOPMENTAL POINT OF VIEW

Lux et al. effectively outline both the importance and the benefits of a developmental framework to a wide range of topics and concerns in contemporary embodiment research, including identifying and providing a nuanced examination of the "transmission hubs" between the multiple levels of activity involved in human development—genetic, epigenetic, cellular, neural, sensory, motor, perceptual, behavioral, social, and cultural. A particular strength of the developmental framework promoted by Lux et al. is that it employs explanatory pluralism to integrate the various approaches currently used in programs of research on embodiment, particularly the *agency* approach and the *environmental* approach. As Lux et al. note, integrating these two research approaches within a developmental framework can provide a range of dividends, including connecting different timescales of embodiment, relating different systems levels to one another, and clarifying disciplinary boundaries. Integrating these approaches can also allow a deeper appreciation of the fact that organisms are both independent and interdependent, are both subject and object, and actively construct their own organization through their actions and exchanges with their environment. As (Overton, 2008, p. 9) succinctly put it, "all development is explained by the action of the individual," where action and experience become synonymous.

In this brief opinion, I focus on two of the many developmental themes that Lux et al. address in their overview of current embodiment research and its potential future directions. The first of these is how to account for the stability and variability of developmental outcomes, a concern of both developmental and evolutionary theory. The second theme has to do with the importance of constraints and how they can contribute to a fuller understanding of the developmental dynamics of embodiment.

Regarding the first theme, as Lux et al. point out, accounting for change and stability from a developmental perspective requires rethinking *process*. From a developmental point of view, the process responsible for phenotypic stability and the process responsible for phenotypic variability are one and the same, namely, the very process of development itself (Lickliter and Harshaw, 2010). This view proposes that the stability of phenotypic outcomes across individuals is found not because of the transmission of genetic programs or the transfer of internal blueprints, but because a range of similar internal and external conditions, collectively conceptualized as developmental resources, are reliably available to developing individuals. Variability of phenotypic outcomes relies on these same developmental resources, but because the internal and external conditions of development are not always the same, phenotypes will also be characterized by at least some variability or change, within and across individuals. Lux et al.' example of the hormonal feed-back loops underlying the stress response established during early development nicely illustrates this dynamic perspective. They note that the set points of up and down regulation of an individual's stress response depend on a range of resources, including the current organization of the nervous system, the individual's metabolic conditions, the specifics of available stimulation, and the nature of the stress experiences encountered during this early period. Although these resulting set points can become relatively stabilized over development, conditions of trauma, hormonal imbalance, or chronic stress can all potentially lead to a change of these set points. In this light, organisms have developed a range of strategies to manage aspects of their own or their offspring's environment to guide and regulate these types of developmental process. This active management, often provided by parental care, allows a degree of dependability of developmental resources during early development, while also allowing for flexibility and adaptability to changing conditions (see Stotz, 2010). For example, rat pups that receive relatively high levels of maternal licking and grooming following birth typically show less physiological and behavioral response to stress throughout the life span than do pups that receive lower levels of maternal grooming during early development (Champagne et al., 2003). Importantly, these patterns can shift when pups are cross-fostered to mothers with different levels of maternal care. In this example, a pup's internal state and its sensitivities are dependent on something outside of it, illustrating the key insight that embodiment is always relational.

A second theme relevant to advancing our understanding of embodiment across the life-span is the notion of constraints. In the most general sense, constraints work by modifying the probability of the occurrence of events and actions. Constraints are relational and simultaneously open up as well as close off possible outcomes (Juarrero, 1999). For example, at all stages of development an individual's body is constrained in its capacities and possibilities of action. Not all movement is possible. Motor activity is both limited and facilitated by the design of muscles and tendons, their flexibility, their relations with other muscles and joints, and their prior history of use. As result, developing organisms, as subjects of their own activity, constrain the dynamics that give rise to and maintain their motor, perceptual, cognitive, and behavioral traits and characteristics. In other words, an organism contributes to its own developmental course by its specific sensitivities, abilities, biases, and previous history, creating its own "effective" environment by the scope and constraints of its own activity in the world. Lux et al.' concern for accounting for gain and loss of function across the lifespan fits nicely into this dynamic perspective.

DISCUSSION

Lux et al. have provided an important addition to the embodiment literature, detailing a framework and heuristic that can take this diverse field into a more integrative and interdisciplinary future. Their well-exampled conceptual analysis of embodiment research and its possibilities for future directions provides a useful road map for how to reduce conflict and enhance communication and collaboration between the various levels and different disciplines involved in embodiment research. As Lux et al. make clear, embodiment research is transforming multiple disciplines across the life sciences and the developmental framework they have proposed provides important conceptual tools to advance this transformation, as well as moving research questions and designs to more deeply and effectively unpack the complex nature of the relations among biological, psychological, and cultural systems involved in human development across the life span.

AUTHOR CONTRIBUTIONS

RL conceptualized and wrote this Opinion.

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The Shared Origins of Embodiment and Development

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As a domain of study centering on the nature of the body in the functioning of the individual organism, embodiment encompasses a diverse array of topics and questions. One useful organizing framework places embodiment as a bridge construct connecting three standpoints on the body: the form of the body, the body as actively engaged in and with the world, and the body as lived experience. Through connecting these standpoints, the construct of embodiment shows that they are not mutually exclusive: inherent in form is the capacity for engagement, and inherent in engagement is a lived perspective that confers agency and meaning. Here, we employ this framework to underscore the deep connections between embodiment and development. We begin with a discussion of the origins of multicellularity, highlighting how the evolution of bodies was the evolution of development itself. The evolution of the metazoan (animal) body is of particular interest, because most animals possess complex bodies with sensorimotor capacities for perceiving and acting that bring forth a particular sort of embodiment. However, we also emphasize that the thread of embodiment runs through all living things, which share an organizational property of self-determination that endows them with a specific kind of autonomy. This realization moves us away from a Cartesian machine metaphor and instead puts an emphasis on the lived perspective that arises from being embodied. This broad view of embodiment presents opportunities to transcend the boundaries of individual disciplines to create a novel integrative vision for the scientific study of development.

Keywords: embodiment, evolution, development, enactivism, experience

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Researchers interested in development occupy niches in various disciplines including biology, psychology, neuroscience, education, and various parts of the social sciences. However, each type of expert spends much of their time viewing developmental questions through a narrow disciplinary lens. We suggest that new insights can be gained by employing the concept of *embodiment* as a wide-angle lens that can reveal novel opportunities for connecting the study of development across a diversity of domains of study. By embodiment, we refer to the nature of the body in the functioning of the individual organism. We follow Overton (2008), who proposed that "Embodiment is a concept of synthesis, a bridge that joins broad areas of inquiry into a unified whole" (p. 3). He further suggested that one way to view embodiment is as a bridge between three standpoints: the form of the body (in the sense of bodily morphology), the body as actively engaged with the world, and the body as lived experience (see also Johnson, 2007).

Here, we take a broad view, framed by the three standpoints of Overton (2008), to highlight how embodiment and development are deeply intertwined, with the hope of encouraging developmental scientists to engage with the implications of an embodied approach. We begin with the evolutionary origins of bodily form and why and how bodies arose. Given that the body does not exist separately from the actions and activities of the individual, we then move to consider the capacity for embodied engagement by the developing organism. The origins of the metazoan (animal) body are of particular interest, given that the evolution of animals involved the emergence of complex bodies with nervous systems and sensorimotor capacities that bring forth a particular sort of embodiment. However, we also emphasize that the thread of embodiment runs through all living things: From single cells, through simple multicellular entities, to the more complex bodies of animals, plants, and fungi, living things share an organizational property of self-determination that confers them with a form of autonomy which is fundamentally different from nonliving things. As such, living systems have a viewpoint or lived perspective that arises through their organization and the nature of their embodiment. This realization moves us away from a Cartesian separation of life and mind and instead puts an emphasis on the embodied perspective of the organism that arises through the nature of the organization of living things. It also underscores how embodiment as a bridge construct can lead to a synthesis of perspectives on the body, challenging us to develop new lines of interdisciplinary developmental research.

THE HOW AND WHY OF BODIES

Although there cannot be a single explanation for why bodies arose, the range of opportunities that emerge from living at a larger scale likely influenced the evolution of the processes involved in the development of bodies. Simply put, the size of unicellular organisms imposes constraints that can only be overcome by becoming multicellular. Sterling and Laughlin (2017) discuss the unicellular eukaryote *Paramecium*, which ingests other, smaller microorganisms, and uses cilia for locomotion. They note that the behavioral repertoire and capacity for learning of Paramecium are limited by its size (0.05–0.30 mm), such that "the cell is still so small that locomotion must be slow, and the environment remains so evanescent that richer behavior and longer memory offer no advantage" (p. 20). From this perspective, greater size is a route towards richer and more flexible behavioral capacities, at the same time allowing access to new niches and energy flows–although this in turn also exposes the organism to new vulnerabilities.

The evolution of multicellularity is a large and complex topic that can only be touched on here. One key distinction is between simple forms of multicellularity such as filaments, clusters, balls, or sheets of cells, and the more complex bodies of animals, plants, and fungi. Simple multicellularity has evolved many times across the domain of eukaryotes, and can even be found in some prokaryotes such as cyanobacteria (Bonner, 1998). What sets more complex bodies apart is that in addition to cells adhering together, there is elaborate intercellular communication, differentiation of cells into different types and tissues, and the involvement of programmed cell death (Knoll, 2011). Behind these general commonalities are important differences in the specific evolutionary and developmental processes that shape multicellularity in animals, plants, and fungi (Niklas and Newman, 2020). For present purposes, the main point is that is that considering the evolution of complex bodies brings the concept of development to center stage. Organisms that exhibit simple multicellularity may show changes across their life cycle, as do some unicellular organisms (Driks, 2002; Huang and Hull, 2017). At some level, such changes may be construed as developmental, although they do not involve the differentiation and integration of multiple types of cell, intricate communication between cells, or the death of cells as part of the developmental process. In this sense, the evolution of complex bodies–which involves all of these characteristics–was the evolution of development itself.

It is notable that the outlines of the physiological processes involved in cell adhesion, cell–cell signaling, and cellular differentiation can be seen in the physiology of unicellular organisms, suggesting that the evolution of development did not involve the wholesale generation of new mechanisms (Grosberg and Strathmann, 2007; Sebé-Pedrós et al., 2017). Recent lines of research have extended this line of thinking to consider how the capacities of single cells can shed light on the building blocks of cognition (Levin et al., 2021; Lyon et al., 2021). We raise these points to emphasize that reaching a deeper understanding of embodiment and development involves a wide-angle outlook that extends across the breadth of living systems, even down to the level of single-celled organisms.

DEVELOPMENTAL AND EVOLUTIONARY PATHWAYS TO COMPLEX BODIES

One key aspect of the development of complex bodies is the differentiation of cells into different types, as parts of bodily subsystems (e.g., tissues and organs) that become integrated in support of the functioning of the whole organism. In turn, the extent of cellular differentiation in a body is tied to increasing size. Many simple multicellular eukaryotes are so small that each cell can be in contact with the external medium, but this is simply not possible in larger bodies. Beyond a certain (very small) size, wider considerations arise around metabolism and transport, which in turn require cells to take on specialized functions (Knoll, 2011; Brunet and King, 2017). In the case of animals, a range of abilities and functions arise through such specialization, including coordinated locomotion, feeding, waste excretion, and reproduction, as well as sensing of the environment–including registering the presence of other organisms.

Understanding the processes that influence the number of cell types in a body is an active area of research (Bush et al., 2017). The differentiation of cells into different types allows bodies to exist at a higher level of complexity than the individual cells of which they are comprised (Michod and Roze, 1997), with the relative complexity of a body reflected by the number of cell types that develop within it (Márquez-Zacarías et al., 2020). Within the realm of animals, some vertebrates may have as many as 250 different types of cells, while animals in basal phyla such as Cnidarians (jellyfish and corals) have far fewer. The pathway to bodily complexification in animals arose in part through the evolution of gastrulation, a series of changes in early embryonic development that gives rise to differentiated layers of cells inside the blastocyst. Although specific details are debated (Nakanishi et al., 2014; King and Rokas, 2017), the evolution of this phase of embryonic development laid the foundation for complex bodies and for the kind of embodiment that accompanies animal life.

Insights into the evolutionary origins of more complex animal bodies can be gleaned from studying basal animal phyla that have relatively simple bodies, without judgements about the nature or value of complexity (Dunn et al., 2015). Cnidarians are particularly informative in this respect: They have some degree of cellular differentiation, have multiple types of tissue within their body, and they have a nervous system, although they lack a brain. They also differ from more complex animals in having radial symmetry, rather than the bilateral symmetry that characterizes almost all other animals. In this respect, it is notable that the bodies of Cnidarians arise from two germ layers (endoderm and ectoderm) that differentiate during gastrulation, whereas more complex animal bodies arise from three germ layers. The evolution of the third germ layer (mesoderm) as a product of gastrulation was associated with a rise in bodily complexity, not only in terms of facilitating an increase in the number of cell types, but also by enabling the development and evolution of major changes in body morphology such as body cavities and bilateral symmetry (Carroll, 2001).

THE ENGAGED BODY

Discussions of the evolution of the animal body often emphasize the important of the “Cambrian explosion” that began around 535 million years ago and left a burst of animal bodies in the fossil record. These bodies were variations on a particular body configuration involving bilateral symmetry (with an anterior and posterior end), segmentation, and specialized appendages. While the origins of this configuration predate the Cambrian, the evolution of the metazoan body shifted animals towards a new way of being in the world. The evolution of animal bodies was accompanied by an increase in the complexity and flexibility in the capacity to act, supported by the evolution of nervous systems, ultimately including brains. As multicellular animals became larger, nervous systems may have first arisen for purposes of internal coordination among cells, prior to the evolution of brains (Keijzer and Arnellos, 2017; Arendt, 2021). Networks of neurons then became incorporated into newly evolving sensorimotor systems that became connected to ways of moving and acting. This connection thus takes us from the first standpoint of bodily morphology to the standpoint of the engaged body and the notion of embodied action.

One key tenet of embodiment is that action is not the “output” of cognitive processing that is part of a stepwise perception-cognition-action sequence. Indeed, the origins of the field of embodied cognition can be traced to dissatisfaction with this mechanical view (Varela et al., 1991). Embodiment presents a distinct challenge to a view of the organism as a passive recipient of “information” with prespecified meaning that is then subjected to computational processing, followed by a behavioral response. Embodied treatments instead emphasize the active nature of the individual organism, with recent accounts focusing on how agency arises through the prospective nature of cognitive processes (Clark, 2013). This emphasis on anticipatory, future-oriented processes takes us from a reactive, feedforward, homeostatic view of organismic functioning to a view in which *allostasis* is the predominant mode (Sterling, 2012). One related emphasis is on the evolutionary primacy of reafferent processes in which sensing the world became intertwined with responsivity to the organism’s own actions (Jékely et al., 2021). A further stipulation of embodiment is that meaning is not prespecified in information that is “picked up” by the organism, but rather that embodied action transforms the objective world into the world that the individual experiences (Overton, 2008). Meaning is therefore shaped by the embodiment of the organism, including the kind of body that it has and the nature and development of its capacities for action (Marshall, 2016).

EMBODIMENT AND THE MEANING IN LIFE

The evolution of complex animal bodies had particular implications for embodiment, with the capacity for more sophisticated action bringing a new way of being in the world. Evolving nervous systems facilitated the coordination and intertwining of moving, sensing, and acting as a single unit, establishing a new kind of “body-self” (Jékely et al., 2021). The distinction between self and non-self became sharper, bringing to the organism a new kind of perspective or point of view. However, although the evolution of the animal body represented a new chapter in the book of embodiment, it did not begin an entirely new volume. By virtue of the particular organizational properties of living systems, the thread of embodiment runs through all living things. This fundamental point features prominently in a line of theorizing around embodiment known as *autopoietic enactivism* that has its origins in the work of Maturana and Varela (1987; Varela, 1979). In turn, this line of thinking has connections to systems-organizational frameworks in biology (Rosen, 1991) as well as to philosophical lines of inquiry that focus on the particular self-determining properties of living things (Merleau-Ponty, 1967).

The autopoietic enactivist view begins from the premise that living things actively self-maintain themselves through the constant regeneration of the conditions that are necessary to sustain their material existence. This organizational feature of life was termed *autopoiesis* by Maturana and Varela, who focused on the individual cell as a unit enclosed by a semipermeable membrane that acts as a boundary between the inside of the cell and the surrounding medium. The inside of the cell is characterized by chemical reactions and transformations that both generate the components of which the cell is composed and maintain the organization of the cell (its boundary and contents) in the face of entropic tendencies to dissolve that organization. What then defines living beings as unities is their autopoietic organization, such that "it is in this autopoietic organization that they become real and specify themselves at the same time" (Maturana and Varela, 1987, p. 48). This self-specification confers on living organisms a particular kind of autonomy that has been termed *constitutive autonomy* by Froese et al. (2007), in contrast to *behavioral autonomy*, where the identity of the system is imposed externally by an operator or observer. There are clear connections here to the teleology of Kant, who proposed that living things exist for themselves in a way that is different from nonliving entities. As framed by Witherington (2014), from the Kantian perspective the living organism "serves as its own cause, organizing and producing itself such that it causes and results from itself. In this way, living systems constitute natural ends or purposes" (p. 27; see also Farnsworth, 2018).

Returning to the framework of Overton (2008), these considerations take us from the standpoints of bodily morphology and the engaged body to the standpoint of the body as lived experience. In short, constitutive autonomy confers the individual organism with a perspective that arises naturally from the organization of living things and the way that this organization comes about. This notion of the organism having an individual perspective then raises questions about phenomenology–questions that have historically been pushed aside by the computational machine metaphor of the organism that originated in the split ontology of Descartes. The machine metaphor does not allow the question of "What is it like to be a living thing?" to even arise. In contrast, embodiment allows us to consider living beings as having what Maturana and Varela called a "biological phenomenology" that arises through their organizational properties. In this view, biological phenomenology does not go against physical phenomenology: There is no split. Maturana and Varela simply propose that as different classes of unities, living beings and nonliving things such as rocks or snowflakes specify particular phenomenologies. The organization that characterizes nonliving unities is not autopoietic, thus precluding them from having a perspective in the sense of the biological phenomenology of living systems that arises through their inherent autopoietic self-specification. This line of thinking remains an important background framework for studying the emergence of agency and autonomy in living systems, including research that probes the interface of mesoscale physical and physiochemical processes that are common to nonliving and living things and agentive behaviors of cellular systems that are unique to living organisms (Arias Del Angel et al., 2020).

IMPLICATIONS FOR DEVELOPMENTAL SCIENCE

In this brief perspective piece, we have outlined a wide-angle view of embodiment that draws together work across developmental and evolutionary biology, developmental psychology, and embodied cognitive science. Considering the evolution of bodies highlights how embodiment is not an add-on to the study of development, but rather that the origins of development are the origins of embodiment. In turn, bodily morphology cannot be divorced from the active agency of the individual, such that embodied engagement of the developing organism comes to the fore. Within developmental science, this emphasis recalls Piagetian notions of schemes that are shaped through assimilation and accommodation, with the process of equilibration moving the developing organism from one world of meaning to another (Di Paolo, 2019). A renewed focus on these ideas, combined with an emphasis on the self-determination of living systems, can return the study of organization and systems to the center of developmental science (Marshall, 2013, 2014). In particular, the interplay between organization (or structure) and process must be deeply considered (Witherington and Heying, 2015). We note that these themes are emphasized in the metatheoretical approach of process-relational developmental systems theory (Overton and Lerner, 2014; Overton, 2015). This approach places embodiment as a core developmental construct, and is founded in a relational worldview that rejects the separation of life and mind that originated with Descartes yet continues to influence contemporary cognitive science.

A further implication of living things as self-determined concerns the perspective of the developing organism. With respect to human development, the view of embodiment outlined here speaks to the importance of an intraindividual, lifespan developmental approach, which still remains to be widely considered in contemporary theorizing. It also leads to a variety of questions about the embodied origins of the self (and self-other relations) and about the development of agency in relation to the construction of embodied meaning (Marshall, 2016). Adopting this multidisciplinary, broad view of embodiment presents distinct challenges, but also provides a valuable opportunity for developmental scientists to transcend the boundaries of their individual fields of study to create a new vision for the scientific study of development.

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Low-Resolution Neurocognitive Aging and Cognition: An Embodied Perspective

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Consistent with embodied cognition, a growing evidence in young adults show that sensorimotor processing is at the core of cognition. Considering that this approach predicts direct interaction between sensorimotor processing and cognition, embodied cognition may thus be particularly relevant to study aging, since this population is characterized by concomitant changes in sensorimotor and cognitive processing. The present perspective aims at showing the value and interest to explore normal aging throughout embodiment by focusing on the neurophysiological and cognitive changes occurring in aging. To this end, we report some of the neurophysiological substrates underpinning the perceptual and memory interactions in older adults, from the low and high perceptual processing to the conjunction in the medial temporal lobe. We then explore how these changes could explain more broadly the cognitive changes associated with aging in terms of losses and gains.

Keywords: embodiment, aging, neurocognition, perceptual processing, conjunction, distinctiveness

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INTRODUCTION

Embodied cognition defines the body and the interaction with the world as shaping cognition and not just as simple inputs/outputs (Wilson, 2002). As a consequence, perceptual and motor systems should play a crucial role in cognitive functioning. Growing evidence, especially in young adults, has shown that sensorimotor components are at the core of language (Pulvermüller et al., 2005), attention (Bradley, 2007), memory (Versace et al., 2014) or action (Hommel, 2009). However, few studies are conducted in normal aging (Vallet, 2015). This is particularly surprising given that aging is marked by perceptual (and motor) decline in the one hand and by cognitive decline in the other hand. This perspective aims at proposing an embodied account of age-related cognitive decline focusing on perceptual and memory interactions in older adults. To this end, the neurophysiological substrates at the origin of the interactions between perceptual and memory should be understood. The low and high levels of sensory neurophysiological changes in older adults will be firstly described as their impact on the emergence of memory representations. Then, with the support of the hierarchical representational model (Murray and Bussey, 1999; Saksida and Bussey, 2010), we will examine how changes in the perceptual-mnemonic conjunctive processes, occurring in the medial temporal lobe (MTL), alter the emergence of representation. Finally, we will discuss how these changes could explain more broadly the cognitive changes associated with aging in terms of losses and gains based on the Activation-Integration model (Versace et al., 2009, 2014).

SENSORY-PERCEPTUAL DECLINE AND LOW-RESOLUTION REPRESENTATION IN AGING

Biological aging affects the whole body including, at a low-sensory level (sensory organs), many sensory modalities. Recently, the five Aristotelian senses (hearing, vision, taste, touch, and smell) was simultaneously assessed in older adults aged 57–85 years (Correia et al., 2016). The results showed that 74% of the participants had a deficit in identifying taste, 70% in touch, 22% in smell, 20% in corrected vision and 18% in corrected hearing. This study also provides for the first time an estimate of the proportion in which the sensory modalities are jointly altered. Two thirds of the participants had a deficit of two or more modalities, 27% had a deficit of only one of these modalities, while only 6% showed no impairment. At a higher level, aging worsens the transmission of sensory information from these organs to the brain (Ulfhake et al., 2002) and higher perceptual thresholds are also found (e.g., Fozard and Gordon-Salant, 2001). At a cortical level, the occipital sensory cortex is less affected in aging with regard to structural integrity (e.g., Peters, 2006), but long-term peripheral sensory alteration may promote atrophy of the perceptual areas of the brain (Baltes and Lindenberger, 1997; Boucard et al., 2009; Golub, 2017). Functionally, the dopaminergic modulation deficit in aging, regulating the neurons sensitivity to related signals, reduces the functional specialization of neuronal activation. This is also true in neuronal circuits that are still relatively intact (Li et al., 2001), especially for visual stimuli in posterior regions (Park et al., 2004). The impoverished perceptual signal results in weakened unisensory and strengthen multisensory information processing (de Dieuleveult et al., 2017). As older adults exhibited reduced activity in occipital regions coupled with increased frontal activity, a functional compensation occurs (Davis et al., 2008).

Embodied cognition predicts that these perceptual changes should directly impact cognitive functioning. In this approach, all forms of knowledge (e.g., semantic, episodic) remains grounded in its sensorimotor components (Glenberg et al., 2013). The cognitive representations are not retrieved in memory, but instead emerge from the simulation of these components associated with the individual's previous experiences based on the constraints of the present situation (**Figure 1**). Simulation refers here to the automatic and mandatory re-enactment of the brain activities of the perceptual, motor and emotional states produced by past experiences in the modal and heteromodal areas (Barsalou, 2008). Thus, the neurophysiological degradation occurring in aging in perceptual processing should deteriorate the simulation mechanism at the core of representation emergence (Vallet, 2015).

A less efficient simulation in older adults should lead to the emergence of "low-resolution" impoverished representations, that is, representations with lower details. In other words, the signal-to-noise ratio of the sensorimotor simulation should be lower, mainly due to a decrease in central perceptual processing. Whereas the perceptual discriminability in memory is underlied by occipital regions regardless of age (Bowman et al., 2019), older adults exhibits reduced representation fidelity in these regions (Zheng et al., 2018). Impoverished sensory input may decrease the activation of specific sensory components of perceptually present information, but it should generally not alter the ability to simulate perceptually absent (and therefore mnemonic) information. Coherently, it has been shown that older adults did not suffer from a retrieval deficit, but insteaded exhibit less precise mnemonic representations of the items (i.e., less accurate responses on the color and orientation) and of the context (e.g., location) of the information to be learned (Korkki et al., 2020). This study also showed that the reduction in accuracy is not fully explained by a deficit in low-level sensory functioning alone (visual acuity), which may rather occur from neural dedifferentiation in the parahippocampus (Koen et al., 2019). The lower-resolution hypothesis could also account for associative (e.g., source memory) deficits in aging. Indeed, older adults have the greatest deficit in access associations requiring a high level of specificity (e.g., the old man was in this park), whereas they performed as well as younger adults to recognize general associations (e.g., the old man was in a park) and fuzzy associations (e.g., the old man was out somewhere) (Greene and Naveh-Benjamin, 2020). As all forms of knowledge (e.g., semantic, episodic, autobiographical) emerges from simulation, a consequence of this hypothesis is that memory deficits in older people should not be limited to newly learned knowledge. Coherently, older adults also recall less specific perceptual or spatiotemporal details in autobiographical memory tasks (very long-term memory see, Frankenberg et al., 2021). A better understanding of the changes requires to study the neurophysiological mechanisms underlying memory in the MTL (the hippocampus and surrounding cortex) and the effect of age on them.

LOW-RESOLUTION REPRESENTATIONS INDUCE MORE INTERFERENCES IN AGING MEMORY

In the MTL, the general coding principle is based on the functional theory of the hippocampus (e.g., Marr, 1971; Rolls, 2013). According to this theory, the emergence of specific memories (i.e., episodic memory) relies on the pattern separation (PS) and the pattern completion (PC) mechanisms. PS is defined as the ability to reduce interference from similar percepts by processing non-overlapping representations, whereas the PC allows recalling a whole and specific memory from an incomplete input signal by complementing (activating) the missing components. The input signals projected from the sensory cortex and then, the entorhinal cortex processed it into a non-overlapping pattern in the dentate gyrus via the mossy fiber (PS). This non-overlapping pattern is then projected as distinct representations into the CA3 field of the hippocampus, after from which the representation could be retried from CA3 by diffusing activation to the cortex (PC, Rolls, 2016; Pishdadian et al., 2020).

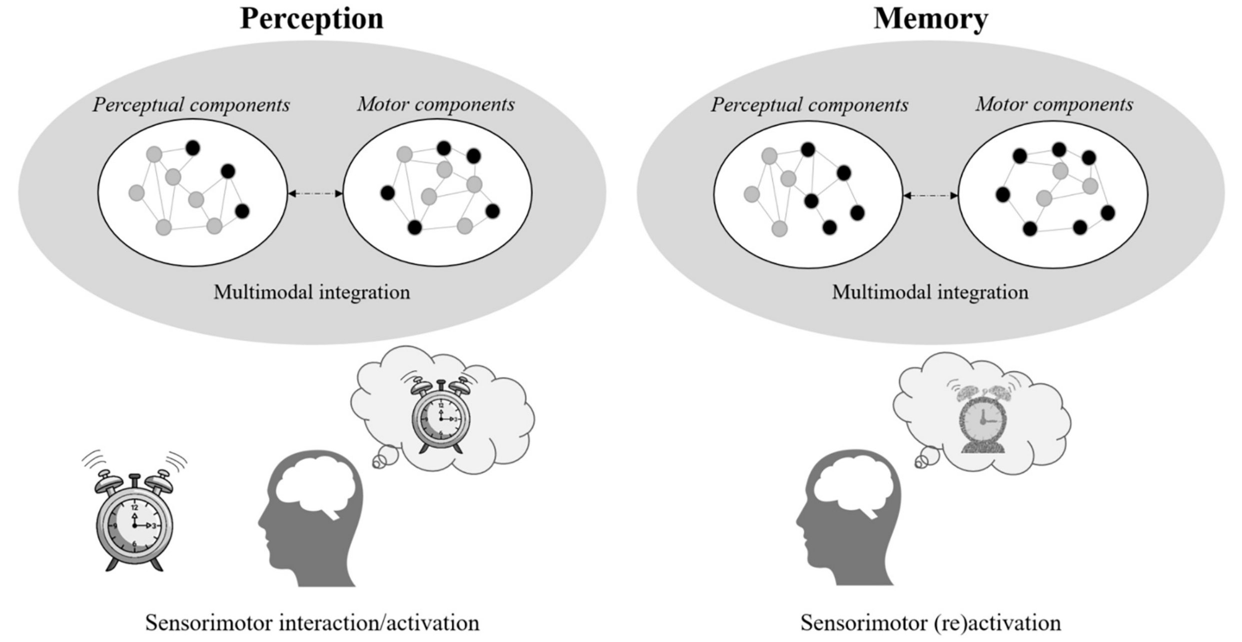

FIGURE 1 | Illustration of the sensorimotor grounded memory traces. The left panel represents the activation of the sensorimotor components when seeing an object (here, an alarm clock). The right panel represents the partial (re)activation, constrained by the present situation, of these sensorimotor components leading to the emergence of the associated memory. As memory is defined as a dynamic emergence, the representation may be slightly different from the percept.

Modern approaches of neurocognition state that PS occurs beyond the hippocampus, all along the ventral stream (Kent et al., 2016; Cowell et al., 2019; Ekstrom and Yonelinas, 2020).

These modern approaches emphasize the content of information to be processed focusing on the visual modality for the moment. All visual representations are, for instance, processed hierarchically from the simplest processing within the visual cortex to the most complex processing in the hippocampus (Murray and Bussey, 1999; Saksida and Bussey, 2010). This representational-hierarchical model states that non-overlapping representations (PS) could be obtained by the conjunction of perceptual features along the ventral stream regions to the hippocampus (see Kent et al., 2016). Basic sensory interference between individual stimulus characteristics (e.g., lines and colors) can be resolved in the sensory cortex. When more perceptually complex features are introduced (e.g., objects), the interference is resolved at higher processing level (e.g., the perirhinal cortex -PrC). Finally, combinatorial codes (e.g., conjunctive representations of object scenes in a spatial context) are resolved in the hippocampus.

The representations are assumed to be widely distributed into a system where characteristics of objects and scenes are progressively combined as the processing progress hierarchically. Moreover, and consistently with the embodiment, memory representation would emerge from the activation of perceptual units, and thus, the distinction between memory and perception are no more relevant (see also, Graham et al., 2010). Thus, conjunctions would not only reduce memory interference, but would also eliminate the ambiguity of visually similar stimuli in supposedly non-memory tasks. Accordingly, the PrC is involved in processing of complex perceptual objects (Buckley et al., 2001; Bussey et al., 2002; Barense et al., 2007) and lesions to the PrC induce false recognition due to interference from similar memories (Burke et al., 2010; McTighe et al., 2010). Similarly, growing evidence indicates that the hippocampus underlies the processing of conjunctions of complex spatial information in memory (Girardeau et al., 2009) and in presumed non-mnemonic tasks (see, Lee et al., 2012).

Applied in aging, the functionally weakened sensory signals in the sensory cortex would increase perceptual/mnemonic interference as conjunctions would be less efficient along the ventral stream. Indeed, and on the contrary to the occipital cortex, the MTL is structurally affected by aging, both in the PrC (Ryan et al., 2012; Fidalgo et al., 2016) and the hippocampus (Fraser et al., 2015). As a result, conjunction processing is expected to be impoverished in older adults. This should increase interference mainly between similar memories (Surprenant et al., 2006; Ekstrom and Yonelinas, 2020). Actually, when the memories are sufficiently distinct (efficient PS or dissimilar memories), then the PC mechanism can easily complete a specific trace, but when the memory traces overlap, then the system will enter into an unstable attractor that may lead to the emergence of altered/confused information (inefficient PC) (Ekstrom and Yonelinas, 2020; Zotow et al., 2020). Furthermore, the contribution of conjunctive representations to reduce interference could be more important as the delay increases. Delay-dependent impairments after MTL damage result from deficient conjunction representations to resolve the ambiguity of simpler representations in lower-level regions that are more likely to be encountered during delay (Yonelinas, 2013). Therefore, the processing of similar information in aging could be impacted at low levels of similarity in long-term memory, while deficits would be evident at shorter time frames (e.g., short-term memory, perception) only at higher levels of similarity.

On a behavioral standpoint, less efficient PS in aging is mainly studied in memory using a *perceptual lure discrimination index*. In a study phase, the participant learns images. In a subsequent recognition task, these images (targets) are presented along with new images that are visually distinct (foils) or that are visually similar (lures) to the targets. The results show a linear decrease in perceptual lure discrimination as perceptual similarity increases in older adults (see Leal and Yassa, 2018). Older adults thus indicated more often having already seen a new image, especially when it is perceptually similar to a target (declining perceptual lure discrimination index). Similarly, false recognition was more likely for items in categories that are visually more similar than those that are more distinct (Boutet et al., 2019). It should be highlighted that the perceptual lure discrimination index is associated with more global cognitive functioning in older adults (Pishdadian et al., 2020). As such, the alteration of the conjunction processing in the MTL could have wider consequences than the specific memories.

DISTINCTIVENESS OF MEMORY TRACES ON OTHER COGNITIVE DOMAINS

The consequence of reduced sensory processing in aging should not be limited to memory according to embodiment. According to the embodied and situated memory models Act-In (Activation-Integration, Versace et al., 2014), representations (e.g., semantic, episodic) emerge from the same sensorimotor components of the different memory traces. All experiences of the individual are supposed to be accumulated as memory traces. These traces are distributed across modal and heteromodal neuronal systems coding the multiple sensorimotor components of the experiences.

The different components of a given memory trace are bound together (Opitz, 2010), following the conjunction processing and therefore the PS. The binding allows the PC, described in Act-In as an intra-trace activation. A specific memory emerges when the activation does not propagate to similar traces (called inter-trace activation). Reversely, the activation of multiple similar traces (inter-trace activation) should produce categorial (non-specific/semantic) knowledge. A strong inter-trace diffusion achieves categorization by eliminating specific details and context of events (see Versace et al., 2009, 2014), mechanism underlined by the CA1 subregion of the hippocampus and neocortical upstream (Kumaran and McClelland, 2012). The intra-trace and inter-trace activations are mutually repulsive so strengthen or weaken one kind of activation should directly weaken or strengthen the other. Given that intra-trace activation is facilitated by distinctiveness, better simulations (higher resolution representations) should allow more activation of contextual details limiting the activation of common/similar components of other traces (inter-trace activation) (e.g., Ekstrom and Yonelinas, 2020). Furthermore, distinctiveness is also a function of the number of experiences accumulated, then more traces should increase the likelihood of their overlap. This, in turn, should increase the inter-trace activation. Consequently, the decline of perceptive and conjunctive processing associated with more traces (more events experienced by older adults) should induce less distinct traces in older adults (Vallet, 2015), then it should in return bias the dynamics of the simulation in favor of the inter-trace activation (less distinct processing).

This balance between specific and non-specific knowledge could be illustrated by the fact that older adults produce fewer internal (specific) details associated with more external (categorial) details when they recall an event compared to young adults (e.g., Levine et al., 2002). The effect of aging on the visual cortex and the hippocampus reduces specific details (neural dedifferentiation), while aging enhances categorial representations in the anterior temporal lobe (neural hyperdifferentiation) (Deng et al., 2021). Therefore, older adults exhibit relatively well-preserved performance in semantic tasks (see, Salthouse, 2010, for a review). However, a more qualitative analysis shows that they produce more categorial (e.g., cat) and less unique (e.g., botfly) semantic knowledge (Murphy and Castel, 2020). Their memory difficulties are then not limited to a given memory system, but rather occur due to the alteration of mechanisms involved in the emergence of specific knowledge. Thus, not only do older adults have less detailed specific knowledge in episodic tasks (specific knowledge, Greene and Naveh-Benjamin, 2020; Frankenberg et al., 2021), but they also less benefit from distinctiveness (see Smith, 2006) due to a more generic (categorial) and less distinct processing (Koutstaal and Schacter, 1997; Smith, 2006).

Aging might be characterized by an imbalance toward generic (non-specific) processing constrained by the weight of prior knowledge at the expense of specific processing. Compared to young adults, older people produced indeed less specific details and more generic details in a basic image description task and in future imagination task (Gaesser et al., 2011; Schacter et al., 2013). Yet, an integrated view of neurocognitive functioning suggests that deficits in modal (e.g., less specialization in occipital processing) and heteromodal (e.g., structural impairment of MTL) regions should alter the processing done within the connected regions as the prefrontal cortex (Davis et al., 2008). The neuromodulation deficit induces noise in the neural processing, including the prefrontal cortex, and leads to less specific and more general processing (Li et al., 2001). As the processes are less specific, and the similarity of the previous processes favors the automation of processes (see Logan, 1988), new processes are less likely to emerge. The same over-repeated processes will more likely emerge, making more rigid and less flexible other processing. This rigidity is found for their executive functions such as to change categorization rules in the Wisconsin tasks (e.g., Daigneault et al., 1992; Ashendorf and McCaffrey, 2008). Interestingly, the largest executive switching costs were found under conditions of ambiguous sensory stimuli and overlap between sets of responses (Mayr, 2001). This is consistent with the hypothesis that perceptual deficits reduce trace distinctiveness and lead to increased inter-trace activation, requiring more inhibition in prefrontal cortex (Li et al., 2001). Similar link between sensory functioning and inhibition is observed in young adults with degraded vision (e.g., cataract vision simulation, as found in pathological visual aging) in the Stroop task (see Monge and Madden, 2016 for a review). A more evidence comes from the Perceptual Lure Discrimination Index in the Mnemonic Similarity Task that is related to inhibition (Foster and Giovanello, 2020). Finally, it is noteworthy that the MocA (global measure of cognitive aging) were associated with lure discrimination performances in older adults (Pishdadian et al., 2020).

CONCLUSION

Normal aging is characterized by sensory-perceptual (and motor) decline, on the one hand, and cognitive decline on the other. Further studies, using a longitudinal design, are required to fully explore the progressive sensory (motor) and cognitive changes occurring throughout life. Embodied cognition provides a theoretical framework explaining the possible these links given that any representation at the source of cognitive functioning remains grounded in these sensorimotor components. As such, memory and perception (and action) are functionally equivalent. This perspective investigated the neurophysiological mechanisms underlying these links. The sensory decline (organ level) should have a minimal impact, mainly on overlapping stimuli by impoverishment of the related signal. Higher perceptual decline should affect the simulation mechanism leading to the emergence of a less specific and detailed representation. Functional changes in the primary perceptual areas may reduce the benefit of distinct perceptual information, while structural changes in the MTL may reinforce of overlapping perceptual and memory information. Since embodied representation should be at the core of cognition, such changes should have wider cognitive consequences than memory. Thus, aging could be characterized by less specific and more rigid processing.

This perspective highlights the interest to study aging in an embodied cognition approach, which could represent an alternative to other theories of cognitive aging due to how the sensory (motor)- cognitive interactions are defined. The focus of the present article on perceptual-memory interactions also suggest that early sensory improvement and environmental enrichment could improve cognitive aging (Leon and Woo, 2018). Similar effects should also be found with motor and action interactions. We hope that this brief overview of the contribution of embodied cognition to characterize neurocognitive aging will encourage further investigation of cognitive functions in aging from an embodied perspective.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

JM: conceptualization, writing – original draft, and project administration. GV: conceptualization, writing – review and editing, supervision, funding acquisition, and resources. SB: writing – review and editing. MI: writing – review and editing, and supervision. All authors contributed to the article and approved the submitted version.

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REVIEW
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Making the World Behave: A New Embodied Account on Mobile Paradigm

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In this review article, we describe the mobile paradigm, a method used for more than 50 years to assess how infants learn and remember sensorimotor contingencies. The literature on the mobile paradigm demonstrates that infants below 6 months of age can remember the learning environment weeks after when reminded periodically and integrate temporally distributed information across modalities. The latter ability is only possible if events occur within a temporal window of a few days, and the width of this required window changes as a function of age. A major critique of these conclusions is that the majority of this literature has neglected the embodied experience, such that motor behavior was considered an equivalent developmental substitute for verbal behavior. Over recent years, simulation and empirical work have highlighted the sensorimotor aspect and opened up a discussion for possible learning mechanisms and variability in motor preferences of young infants. In line with this recent direction, we present a new embodied account on the mobile paradigm which argues that learning sensorimotor contingencies is a core feature of development forming the basis for active exploration of the world and body. In addition to better explaining recent findings, this new framework aims to replace the dis-embodied approach to the mobile paradigm with a new understanding that focuses on variance and representations grounded in sensorimotor experience. Finally, we discuss a potential role for the dorsal stream which might be responsible for guiding action according to visual information, while infants learn sensorimotor contingencies in the mobile paradigm.

Keywords: mobile paradigm, sensorimotor contingency, embodiment, infant memory, learning

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INTRODUCTION

Throughout the first half of the 20th century, young infants were viewed as unformed versions of adults whose learning capacities were limited due, in part, to underdeveloped prefrontal structures (Hodel, 2018) and a lack of language (McGraw, 1932; Twitchell, 1965). Rovee-Collier was one of the pioneers against the idea that young infants are not able to learn (Branson, 2014). One day, while trying to stop her son from crying to study for her dissertation exams, she made a profound observation, one that would define her academic career. Her 1.5-month-old son had a mobile that she always used to distract him. On that day, she remembered her grandmother's saying, "Oh, darling, if you could only harness the energy of a 2 or 3-year-old to run the windmills in Holland" (Rovee-Collier, 2006, p. 8), and thought that she could test this claim. She tied the silk belt on her dress to the mobile and the infant's foot, so that whenever her infant moved his leg, he would activate the mobile. She observed that her son increased his kicking rate when his leg was tied to the mobile and stopped kicking when it was not. The observation of her son's behavior led her to test the idea that young infants could learn new behavior by adjusting their actions to gain a reward. The results were remarkable: 2-month-old babies doubled, and in some cases tripled, their response rate in the first couple of minutes of the acquisition phase (Rovee and Rovee, 1969). However, they were also controversial. Reviewers noted that the topic was not interesting, as infant motor actions were recognized as "something a cockroach could learn" (reviewer response as reported by Rovee-Collier, 2006, p. 16) and at odds with contemporary theories ("these are wonderful data, but we do not believe them, because Piaget said babies can not do this"; Rovee-Collier, 2006, p. 9). Despite these arguments, the first article was eventually published (Rovee and Rovee, 1969), followed by more than 100 others using her invention, the mobile paradigm.

For more than 50 years, the mobile paradigm was used to study a wide range of topics, from perceptual abilities to the long-term memory capacity of young infants, challenging contemporary views on the capabilities of and learning opportunities available to young infants. Although a recent article (Jacquey et al., 2020a) reviewed the literature on contingency learning paradigms, including the mobile paradigm, to examine different determinants affecting learning sensorimotor contingencies, no review has yet attempted to integrate the entire range of studies using the mobile paradigm from Rovee and Rovee (1969) to today (Jacquey et al., 2020b; Zaadnoordijk et al., 2020). Additionally, the present review discusses a role for a new account on the mobile paradigm by offering a critical perspective on some aspects of this literature. In this article, we aim to review studies that have relied on the mobile paradigm to assess learning, motor development, memory, and cognition in early infancy, starting with a description of the core mobile paradigm itself and ending with presenting a different interpretation of the paradigm, one that focuses more on the embodied experiences of the infant and her movements.

THE MOBILE PARADIGM

The mobile paradigm is an operant conditioning procedure implemented by Rovee-Collier so that she could study infant memory development (for a detailed review of methods used to investigate infant memory see Rovee-Collier and Hayne, 1987; Hayne, 2004). In this procedure, the rate of stimulus presentation in response to the behavior is determined by a conjugate reinforcement schedule in which the reward is proportional to the amount of behavior exhibited (Lindsley, 1957; Rovee and Rovee, 1969). In Rovee-Collier's (1996) terms, it allows the infant to shop for the value of the reinforcing stimulation they most prefer.

In practice, the procedure is as follows. After the infant is placed in a crib, a ribbon is attached to one of their legs. Two adjacent stands are mounted on the crib, one connected to a mobile phone, and the other is empty. The original (and most used) paradigm has three phases: baseline (3 min), acquisition (9 min), and extinction (3 min; Fagen et al., 1976; Sullivan et al., 1979). During the baseline and extinction phases, the infants are allowed to move their legs normally with their legs attached to the empty stand. During the acquisition phase, the leg is connected to the mobile stand and their movements set the mobile in motion. Rovee-Collier argued that, after operant learning took place (e.g., increased kicking rate in the first minutes of acquisition phase) by gaining control over the mobile, the environment continued to reward the infant, resulting in individual differences in movement with respect to how much the infant experimented with their surroundings. Not only the sensory consequences (e.g., haptic feedback in the leg, visual stimulation coming from the moving mobile), but "making the world behave" (Skinner, 1953, as cited in Rovee-Collier and Gekoski, 1979), in other words gaining control over the mobile, strengthened the stimulus-response associations.

BREAKING THE GROUNDS

These ideas contradicted the prominent theories of the time. For example, Piaget (1952) observed his 2-month-old son Laurent while he was moving his arms connected to the toys hanging above his crib and interpreted these actions as expressions of joy, not as conscious coordination. Furthermore, Piaget (1952) thought that infants at this age can not be operantly conditioned (as cited in Rovee-Collier and Barr, 2001). For Rovee-Collier and Gekoski (1979), however, a similar type of behavior in the mobile paradigm indicated voluntary actions learned through reinforcement rather than increased excitement. The evidence supporting their argument demonstrates that the increased movement was specific to the limb connected to the mobile and did not occur in other limbs, contrary to the joy-based interpretation (Rovee-Collier et al., 1978). Also, when the ribbon was initially connected to one leg and then switched to the other, the learning pattern reversed. In other words, infants increased the kicking rate of the currently attached leg and decreased the kicking of the previously reinforced leg. These results revealed two important conclusions: neither proprioceptive feedback nor a joy reaction could explain the increase in kicking in the leg connected to the mobile, and young infants could adapt to their changing environment quickly and adaptively. Rovee-Collier (1996) interpreted this as an indication that infants prefer cost-effective actions to minimize their energy consumption.

EXTENDING THE PARADIGM

After the original mobile paradigm showed that young infants can learn a new motor behavior through operant conditioning (Rovee and Rovee, 1969; Rovee-Collier et al., 1978), the extensions of the original paradigm were developed for investigating learning and memory early in infancy. For instance, Watson (1979) conducted series of experiments where a pillow under the infant's legs triggered the movement of the mobile. It was shown that the learning rate was differentially affected depending on the changing probability of non-contingent as well as contingent stimulation. Other extensions of the mobile paradigm were used for studying infant memory: a test of simple forgetting and reminder procedures (for a detailed review see Rovee-Collier and Hayne, 1987; Rovee-Collier and Barr, 2001).

Test of simple forgetting measures retention, or how long information can be maintained in memory, which has been shown to range from a day to a week (Rovee and Fagen, 1976; Sullivan et al., 1979). In this test, memory is measured by reintroducing the infants to the training mobile after a retention interval. Two measures are used to estimate the amount of retention: baseline ratio and retention ratio. The baseline ratio indicates whether the response rate in the long-term retention test exceeds the baseline movement level. The retention ratio describes how much the infant's response rate in the long-term retention test differs from the response rate in the immediate retention test that occurs immediately after the learning is complete. Forgetting rates of infants following the learning is determined by measuring retention ratios in different groups at varying retention intervals. This group-level analysis enabled the mapping of the timeline of forgetting in young infants (**Figure 1**).

There are two types of reminder paradigms, referred to as reactivation and reinstatement. The reactivation paradigm measures retention after longer intervals of up to several weeks by introducing a reminder after the memory is forgotten (i.e., when it becomes inaccessible). During reactivation, infants are reminded by the cues from the training episode by passively viewing a moving mobile between the training and test sessions to make a dormant memory accessible again (Rovee-Collier and Hayne, 1987). In the reinstatement paradigm, infants can move the mobile in the reminder session that occurs again between the training and test sessions (Borovsky and Rovee-Collier, 1990; Galluccio and Rovee-Collier, 1999; Adler et al., 2000). Though infants passively observe the mobile in the reactivation paradigm, reinstatement allows them to actively participate in the reminding.

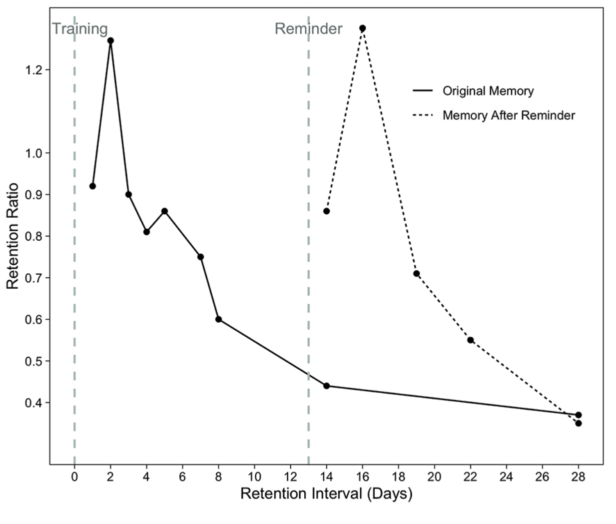

FIGURE 1 | Retention ratios after 2 days of training (solid line) or 2 days of training plus a reactivation reminder (dashed line). Redrawn from Rovee-Collier and Sullivan (1980). Copyright (1980) The American Association for the Advancement of Science.

MEMORY

In the mid-20th century, the field of psychology went through a major transition period, but infant memory was not an often-studied phenomenon. Until 1965, the word memory was not even mentioned in Child Development abstracts (Kail and Hagen, 1977, as cited in Miller, 2014). At the time, behaviorism was the prevailing theoretical account for studying learning and memory, but the cognitive revolution was starting to change the field (Miller, 2003). Behaviorist accounts argued that the building blocks of learning and memory are stimulus-response associations. However, more cognitivist ideas of memory in general, and memory development, in particular, were emerging. For example, Tulving's differentiation between semantic and episodic memory (Tulving, 1972) was one of the ground breaking ideas of the time that reconceptualized memory formation as more nuanced and complex than what was expected from reinforcement accounts. Similarly, new ideas about memory, such as context effects (Tulving, 1972; Tulving and Thomson, 1973; Godden and Baddeley, 1975), and the susceptibility of memories to change when encountering new information (Loftus, 1975, 1979) were emerging. Inspired by these ideas and taking an active role in the transformation of psychological science, Rovee-Collier carried out systematic investigations of these phenomena in early infancy, but her early work was still firmly grounded in behaviorism.

In their seminal article, Rovee and Rovee (1969) claimed that young infants can be operantly conditioned, as 3-month-old infants tripled the kicking rate within the first couple of minutes of the acquisition phase when the mobile was connected to their leg, assuming that the movement of the mobile reinforced the infants' kicking. After successive days of training with the same mobile, infants remembered the same mobile 1 week following the training (Sullivan et al., 1979) and discriminated against a novel mobile (Fagen et al., 1976; Rovee and Fagen, 1976). These findings were the first to provide evidence that young infants can remember learned information after intervals far longer than previously assumed, meaning that young infants could store learned information for days, not only a couple of hours (Fagan, 1970, 1971). The retention capacity of young infants was found to increase with age, from 1 week at 2 months old (Vander Linde et al., 1985) to 13 weeks at 18 months old (Hartshorn et al., 1998a; Rovee-Collier and Hartshorn, 1999).

Using the reactivation paradigm, Rovee-Collier and her colleagues demonstrated that 2–3-month-olds can retain learned information for at least a couple of weeks when they were reminded between training and test sessions (Rovee-Collier et al., 1980; Fagen and Rovee-Collier, 1983; for a review see Rovee-Collier and Hayne, 1987). Observing the non-contingently moving mobile as a reminder (reactivation paradigm) increased the probability of remembering the training mobile to a degree that it would be remembered at the end of the training episode when the memory was just formed (Rovee-Collier et al., 1980, **Figure 1**). This suggests that, not only forgetting can be recovered due to a reminder, but also that the reminder leads to retention of memory as complete as just after training. Forgotten memories were recovered more quickly as infants got older, 24-times faster at 6 months of age compared to 3 months of age (Fagen and Rovee-Collier, 1983; Boller et al., 1990; for a review see Rovee-Collier and Hartshorn, 1999). When the infants were reminded periodically by activating the mobile themselves (reinstatement paradigm), both 3- and 6-month-olds remembered the training memory for 5 months (Rovee-Collier et al., 1999) and 18 months, respectively (Hartshorn and Rovee-Collier, 1997, as cited in Rovee-Collier and Hartshorn, 1999).

Together, these studies revealed the remarkable memory capacity in early infancy, which is taken for granted in the current understanding of development. Furthermore, they have a clear theoretical implication because they support the argument for a distinction between availability and accessibility in memory of young infants, which was initially discussed as a characteristic of adult memory (Tulving and Pearlstone, 1966; Tulving, 1972). According to this distinction, a failure to remember learned information may indicate that the trace of the memory is lost and the memory is not available anymore, or a failure to access the information stored in the memory. The forgetting of young infants was considered an accessibility failure rather than encoding or storage deficit because of their capacity to remember what they learned when they were reminded (Rovee-Collier and Hayne, 1987). Similarly, the memory performance of 2-month-old infants was not different from their older counterparts when they were given the opportunity to encode more cues during encoding (Vander Linde et al., 1985; Hayne et al., 1986). Therefore, even 2-month-olds could overcome the quick decay by sampling more cues during encoding, which is in sharp contrast to the idea that young infants are unable to retrieve stored information due to the immaturity of the central nervous system (Campbell and Spear, 1972) or long-term memory that has not been fully formed (Kagan and Hamburg, 1981, as cited in Schacter and Moscovitch, 1984; Olson and Strauss, 1984; Schacter and Moscovitch, 1984).

TWO DISTINCT MEMORY SYSTEMS

In the 1980s, research on adult memory pointed to dissociations between two memory types depending on whether the recollection of memory is a conscious process, mostly referred to as implicit and explicit (Graf and Schacter, 1985), or declarative and non-declarative (Cohen and Squire, 1980). The evidence for such a dissociation derived from amnesic patients' impaired performance on explicit, but not implicit, memory tasks, and the two memory systems' differential susceptibility to previous experience or priming (for a review see Schacter et al., 1993). Schacter and Moscovitch (1984) argued that such differentiation was not evident in the first 6 months of life, and memory that requires conscious recollection (also referred to as late maturing memory system or explicit memory) develops towards the end of the first year. On the other hand, Rovee-Collier (1997) argued that the test of simple forgetting and the reactivation paradigm measure two distinct memory systems that are fully functional even in the first months of life. An important example of such memory dissociation in young infants is the development of explicit memory with age, as measured with the simple forgetting test, whereas implicit memory capacity (e.g., reactivation paradigm) remains the same throughout development (Hartshorn and Rovee-Collier, 1997; Rovee-Collier, 1997).

The studies discussed so far provide evidence that, even at 2 months of age, infants have a remarkable capacity for learning sensorimotor contingencies and retaining what they have learned for days, and in some cases even weeks when they are reminded using cues from the training episode. Maturation has a role in memory development, as the retention capacity increases with age, but experience also impacts the extent to which young infants remember what they learned days before. When the opportunity is given to encode more cues during training, young infants' long-term memory is expanded, suggesting that the forgetting of young infants is not an availability issue, but an accessibility failure. In summary, infant memory is not an unformed version of human development but is recognized as a critical aspect of development with functional similarities to adult memory.

TIME WINDOWS

Rovee-Collier introduced the concept of time windows to identify the critical periods when different events or pieces of knowledge are integrated (for a review see Rovee-Collier, 1995). After encountering a piece of information, if a new encounter occurs outside the critical time window (e.g., 4 days after the initial encounter at 3 months of age, Rovee-Collier et al., 1993a), these two instances are perceived as two separate events or representations. If the new encounter occurs within 4 days following the first encounter, then these two events are integrated and formed one memory representation. The integration of two temporally distinct events may have a wide range of outcomes, such as learning (Rovee-Collier et al., 1995), forming and expanding category representations (Rovee-Collier et al., 1993a), memory modification (Rovee-Collier et al., 1994; Boller et al., 1995; Muzzio and Rovee-Collier, 1996) and retrieval success (Rovee-Collier et al., 1980; Greco et al., 1986). An important example of the role of learning and memory is that, if the time interval between the first and second training session was less than 3 days, these two event representations were integrated and the training mobile was remembered for the next 8 days (Rovee-Collier et al., 1995). On the fourth day, however, the time window closed and the infant did not remember the training mobile at the 8-day retention test (**Figure 2**).

Modification of prior memories is another function of the time windows. For instance, when adults are presented with conflicting or misleading information after an event, their memory of the previous event could change drastically (Loftus, 1975, 1979). Being exposed to post-event information could also change the memories of young infants if the exposure is

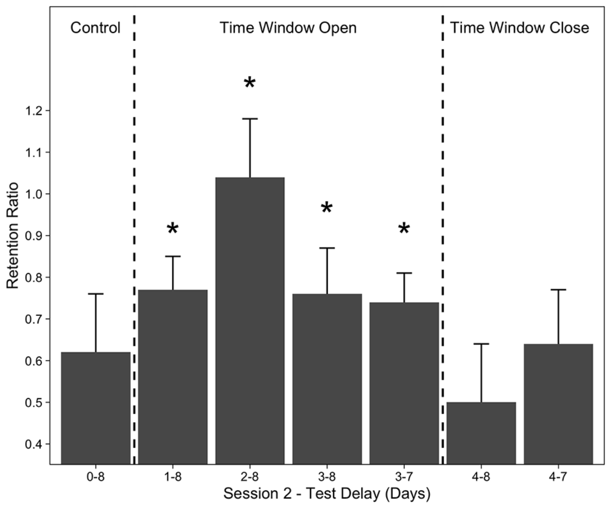

FIGURE 2 | Mean retention ratios of 3-month-olds whose second training session followed their first by either 1, 2, 3, or 4 days and control group who received no second training session. Asterisks indicate that groups whose second session occurred within 3 days of Session 1 exhibited significant retention. Error bars represent ±1 SE. Redrawn from Rovee-Collier (1995). Copyright (1995) Elsevier.

within a certain time window. After training with the same mobile for consecutive days, infants who encountered the novel mobile after less than 3 days remembered both the training and novel mobiles in the future (Rovee-Collier et al., 1994). A more than the 3-day interval between training and post-event information (novel mobile) resulted in disruption of the training memory. Infants only remembered the mobile presented as post-event information. At 6 months of age, when the post-event information (novel mobile) was presented immediately after training, infants still remembered both memories of the training and novel mobile (Boller et al., 1995). However, after intervals of more than a day, the infants did not remember the training mobile anymore (Muzzio and Rovee-Collier, 1996). Taken together, these studies support the idea that memories of young infants are also integrated with novel information in a way that both representations are intact only if the post-event information is encountered within a specific time window. Outside of this time window, only recent events are emphasized, at the cost of prior experiences. Infants could update their behavior when the memory of prior experiences becomes fuzzy with time and, in that case, new sensory information is weighted more heavily in the final memory representation.

The evidence presented in this section suggests that the time window is an important cognitive construct in early development and indicates when infants integrate separate events or representations to form category representations, to enhance long-term memory, and to be reminded of previous encounters. According to Rovee-Collier (1995, p. 166) time windows are the "mortar that holds together the separate building blocks of cognitive development." In these critical periods, subsequent encounters could not only facilitate the memory of an event but also alter it. Given that the focus of these findings is a group-level analysis of the behavior of young infants, what is now needed is an investigation of individual differences in time windows and how these differences are important for later cognitive functions (e.g., intelligence and working memory). Overall, forming memories of past events is a time-sensitive process, and frequent exposures to the elements of the original event support long-term memory consolidation during early infancy.

GENERALIZATION AND VISUAL CONTEXT

Young infants encode not only the proximal cues, such as the mobile itself, but also distal cues, such as the bumper in the crib and the room in which the learning occurs to function as effective reminders in the future (Rovee-Collier et al., 1985; Rovee-Collier and Hayne, 1987; Hayne et al., 1991). For example, when they encountered the same crib bumper as in the training, this familiar cue helped them remember the training mobile (Fagen et al., 1976; Hayne et al., 1986). In addition to the visual features of the environment, correlated attributes of these features (e.g., red block always presented with "+" figure on the block) are learned by young infants (Bhatt and Rovee-Collier, 1994, 1996, 1997). When these features are highly distinctive (e.g., unfamiliar and colorful liner in the crib presented to infants), they showed significant retention for the specific details of the learning episode at 3 months (Butler and Rovee-Collier, 1989) and 6 months of age (Boller et al., 1990). Similarly, distinctive local features on a block of the mobile among distractor blocks (e.g., Q figure among O figures and R figure among P figures) created a pop-out effect, resulting in better retention due to in-depth processing (Adler et al., 1998a,b; Gerhardstein et al., 1998, 1999; Rovee-Collier et al., 1999). Furthermore, both the auditory context created by playing the same musical piece (Fagen et al., 1997) and the olfactory context in which infants smelled the same ambient odor (Rubin et al., 1998; Schroers et al., 2007; Suss et al., 2012) helped infants remember the mobile that they encountered days before if these contexts were shared between the training and test sessions. As a result, retention in early infancy is significantly facilitated by the availability of cues only if the test session consisted of the cues from training. These results are in line with the argument that an event is more likely to be remembered when the learning and retrieval episodes are highly similar, which refers to the principle of encoding specificity introduced in adult memory research by Tulving (1972). Moreover, a specific visual characteristic of the environment such as distinctiveness of the visual context (e.g., linen draped over the crib) and stimuli (e.g., pop-out block in the mobile) could enhance the retention.

The visual cues that are incorporated into memories can help infants generalize their response to another mobile encountered in the future (Fagen et al., 1984; Hayne et al., 1986). For example, 3-month-old infants responded at the same rate of kicking as in the training when they were tested with the novel mobile 4 days after the training ended only when the general features of the memory remained and the specific features were forgotten (Rovee-Collier and Sullivan, 1980). Another similar generalization effect has been observed when infants are presented with multiple different mobiles during training (Fagen et al., 1984; Hayne et al., 1987; Greco et al., 1990; Rovee-Collier and Dufault, 1991; Rovee-Collier et al., 1993a,b; Merriman et al., 1997). In a more recent study, 3–4-month-old infants generalized their kicking response to a test mobile when the toys faced the infant from an angle different than the wide range of viewpoints available in the training mobile (Kraebel et al., 2007).

There are also cases in which the memory of the training and cues in the test session differ so that young infants' response level returns to baseline, suggesting that they distinguished subsequent cues from the memory of the training. The visual cues facilitated the novelty detection when a novel mobile was presented after the training with the same mobile over successive days (Rovee and Fagen, 1976; Rovee-Collier and Sullivan, 1980; Fagen et al., 1984), the number of toys in the mobile decreased from training to test (Mast et al., 1980), and local features (color and shape) of the linen draped over the crib was different during the long-term retention test (Rovee-Collier et al., 1992). Thus, infants distinguish an encounter that differs from what they learned in the past because their memories also help them create expectations for future events (Mast et al., 1980; Fagen et al., 1984; Fagen, 1993). Violation of these expectations (e.g., number of toys decreased from 10 to 2) resulted in crying and fussiness (Fagen and Ohr, 1985; Singer and Fagen, 1992). This negative reactivity also disrupted the retention for the learned mobile a week later (Fagen et al., 1985, 1989).

Infants' ability to learn and retain memories along with the information about where an event took place (e.g., visual context information, a place where the experiment is held) contradicts the ideas of the time claiming that the retention capacity for place information is limited in the first year of life due to the immaturity of the hippocampus (Nadel and Zola-Morgan, 1984). The argument that the retention capacity for declarative memories develops towards the end of the first year of life was supported recently (Bauer, 2006, 2008), and it was still considered the dominant view concerning infant memory (Mullally and Maguire, 2014). Recent arguments against the late maturation of the memory system have been provided by Hayne (2004). Variables that influence the declarative memory performance of adults, such as age, length of the retention interval, and whether the context changed from training to test, have been argued to also affect the memory performance of young infants in the mobile paradigm, suggesting that higher-order memory skills that require conscious recollection as in declarative memory exist in young infants. The lack of consensus in this long debate highlights that targeted research on the development of explicit memory in early infancy is needed to resolve the issue.

All of the studies reviewed in this section suggested that the memories of young infants consist of global and local visual cues of their immediate surroundings. Depending on the extent to which the cues of the environment and memory are compatible, infants either detect the distinctive features or generalize their response, and violation of their expectations of the consequences of the task may result in negative emotionality.

SUMMARY OF ROVEE-COLLIER'S WORK ON MOBILE PARADIGM

When Rovee-Collier started her systematic investigation of infant memory, young infants' capacity for encoding and retrieving information was considered to be quite limited (Nadel and Zola-Morgan, 1984; Schacter and Moscovitch, 1984). In contrast to these ideas, research on infant memory conducted by Rovee-Collier and colleagues argued that infants have a capacity for learning visual cues and the context surrounding them (Rovee-Collier et al., 1985; Hayne et al., 1986; Butler and Rovee-Collier, 1989; Hayne and Rovee-Collier, 1995; Hartshorn et al., 1998b). The infants gradually forget what they learned (Rovee-Collier and Sullivan, 1980; Rovee-Collier et al., 1981; Boller et al., 1990), but remember for a long time when they are reminded with effective cues (Rovee-Collier et al., 1980; Fagen and Rovee-Collier, 1983; Galluccio and Rovee-Collier, 1999), and their memories are modified by encountering novel information (Rovee-Collier et al., 1993a, 1994; Boller et al., 1996; Muzzio and Rovee-Collier, 1996). Although some developmental differences have been observed concerning the temporal parameters of these basic memory processes (Fagen and Rovee-Collier, 1983; Boller et al., 1990), Rovee-Collier and colleagues claim that the same principles apply to the memory systems of both infants and adults (Rovee-Collier, 1997; Rovee-Collier and Hartshorn, 1999; Rovee-Collier and Barr, 2001). These findings are in line with the idea that pre-verbal infants' memory capacity is more than just habit or motor learning (Meltzoff, 1985; Nelson, 1995; Thelen, 2000; Hellmer et al., 2018). They are also in parallel to the results of other declarative memory measures (e.g., imitation task) that were used to study the memory capacity of pre-verbal infants (Meltzoff, 1985; Bauer and Mandler, 1989). For instance, studies with both imitation tasks (Bauer, 2015) and mobile tasks (Boller et al., 1990) showed that how long the memory will be remembered increases with age. Likewise, the serial order of the events/actions are learned in both of these tasks (Gulya et al., 1998; Carver, 1999).

RECENT YEARS

The recent literature which grew outside of the work by Rovee-Collier and colleagues has taken the sensorimotor experience into the center by investigating how the ability to learn sensorimotor contingencies can answer questions about motor and cognitive development at large. This section first gives a brief overview of recent research that has focused on mechanisms underlying learning sensorimotor contingencies and their possible cognitive outcomes. We then review the literature on motor development, more specifically research that used the mobile paradigm as a way of understanding the ontogeny of motor behavior.

Emerging findings shed light on possible learning mechanisms that may be at work while learning sensorimotor contingencies in the mobile paradigm (Kelso and Fuchs, 2016; Kelso, 2016; Zaadnoordijk et al., 2018). Some findings based on computer simulations show that increased movement in the contingent phase could be explained by reinforcement learning that does not require any representation of the cause and effect relationship (Zaadnoordijk et al., 2018). Earlier accounts of learning in the mobile paradigm were in line with this argument. Operant conditioning was considered the underlying learning mechanism, and movement of the mobile was considered to function as the reinforcer, leading to the gradual increase in the movement rate (Rovee and Rovee, 1969; Fagen et al., 1976; Hayne, 2004). Both gaining control over one's actions (Rovee-Collier and Gekoski, 1979) and the context constituting the visual aspects of the infant's environment (Rovee-Collier et al., 1985) contributed to the reinforcement value of the moving mobile. This interpretation differs from that of Kelso (2016), who asserted that, in the mobile paradigm, the infants realize that they can change the environment with their own movements and, therefore, can infer causality from the relationship between the actions and their consequences. Empirical investigations into the role of causal learning on the mobile paradigm have examined whether infants' expectations are violated when the movement of the mobile is not contingent upon their actions (Zaadnoordijk et al., 2020). When the mobile was disconnected, electroencephalography showed mismatch negativity pointing to violation of expectation, along with a movement burst in the connected limb, suggesting that the infant's predictions of the cause and effect model were violated. Despite being few and without consensus, these findings provide important insights into the role of learning sensorimotor contingencies in the mobile paradigm on infant cognitive development. Further research could benefit from modeling empirical data to examine how these learning mechanisms differentially affect detecting and remembering the contingent relationship between infants' actions and their consequences.

To date, several studies have examined the kinematics of movement in the mobile paradigm to shed light on how motor development is affected by the infants' interaction with the environment (Watanabe and Taga, 2006, 2009, 2011; Watanabe et al., 2011). Some other researchers were specifically interested in the movement patterns when the mobile paradigm had specific task requirements. In these experimental designs, only the movements that satisfied particular criteria, such as the angle between the upper and lower leg exceeding a threshold (Thelen, 1994; Angulo-Kinzler and Horn, 2001; Angulo-Kinzler, 2001; Angulo-Kinzler et al., 2002; Tiernan and Angulo-Barroso, 2008), keeping the foot (Sargent et al., 2014, 2015) or head (Tripathi et al., 2019) above a virtual threshold, and foot contact with a touch panel (Chen et al., 2002), were able to activate the mobile. For example, Angulo-Kinzler (2001) developed the constrained version of the mobile paradigm in which the legs of the infants activated the mobile only if the extension or flexion of the leg exceeded a particular angle threshold. Though some infants executed small movements around the threshold without increasing the overall movement rate, others preferred large extensions and flexions that resulted in increased movement frequency (Angulo-Kinzler and Horn, 2001; Angulo-Kinzler et al., 2002). As a result, infants not only increased the movement frequency while learning the contingency in the mobile paradigm but also developed unique and adaptive motor solutions according to the task requirements, suggesting a role of individual differences in learning sensorimotor contingencies.

Recent technological developments enabling more sensitive measurements have led to a renewed interest in individual differences in the learning and retention abilities of infants in the mobile paradigm. Given that previous reports have indicated that not all infants can learn the contingency in the mobile paradigm (Gerhardstein et al., 2012; Jacquey et al., 2020a), investigating behavioral differences between learners and non-learners has gained importance. In a study in which the mobile was activated only if the target leg exceeded a virtual threshold, infants who were able to learn the task exhibited different movement kinematics (e.g., less in-phase hip-knee coordination) compared to non-learners during the acquisition phase (Sargent et al., 2015). In another study in which the infants were required to move their heads above a virtual threshold, 50% of them did not satisfy the learning criteria (Tripathi et al., 2019). During the acquisition phase, learners increased the amount of time that they reactivated the mobile by exceeding the virtual threshold with their heads, whereas non-learners maintained their baseline level. Similarly, Watanabe and Taga (2011) demonstrated that infants whose average arm movements had high velocity during baseline did not increase their movement rate in the acquisition phase, whereas infants with low-velocity arm movements increased their overall movement rate, suggesting that they were able to detect the causal relationship between their arm movements and the movement of the mobile. Overall, individual differences in the movement characteristics of the infants (e.g., velocity of the limbs) are related to whether infants can learn the contingency between their actions and consequences.

How these individual differences predict later motor and cognitive development has also received some attention. For example, a longitudinal study demonstrated that immediate retention capacity in the mobile paradigm is related to motor development, verbal skills, and intelligence at 24 and 32 months of age (Domsch et al., 2009). Similarly, the amount of reaching increased at 3 months of age when infants were trained with a mobile contingent upon their arm movement, suggesting that sensorimotor learning could facilitate the development of other motor behaviors (Needham et al., 2014). The intriguing question of how learning and remembering sensorimotor contingencies affect future behavior can be explored usefully in further research, especially when the limited number of longitudinal studies on this topic is taken into consideration.

Using the mobile paradigm, researchers have also been able to investigate how different age groups and populations differ in terms of their motor behavior while learning sensorimotor contingencies. Watanabe and Taga (2006) argued that, from 2–4 months of age, the motor behavior of young infants follows a general to a specific trend. More specifically, 2-month-old infants increased the movement frequency of all limbs during the acquisition phase, and movement increased in the specific arm connected to the mobile only at 4 months. Similarly, limb differentiation was observed in infants aged 4–8 months in a contingency detection task in which the presentation of an audio-visual stimulus was contingent on the movement of a particular arm (Jacquey et al., 2020b). Despite the failed attempt of Jacquey et al. (2020b) to replicate the developmental trend observed in Watanabe and Taga (2006), both studies showed that the limb differentiation started at 4 months of age. Previous results reported by Rovee-Collier et al. (1978) showed that such limb differentiation is evident even at 3 months. The most obvious conclusion to emerge from these studies is that learning in the mobile paradigm is not the result of a joy reaction (Piaget, 1952) because infants can increase the movement of a particular limb while keeping the others at the baseline level. However, it is also important to note that age-related differences concerning such limb differentiation are inconclusive, and one likely explanation may be that the methodological parameters varied among studies. For example, Watanabe and Taga (2006) used a motion tracking system to analyze the movement of infants, and Jacquey et al. (2020b) measured the arm activity with accelerometers, whereas Rovee-Collier et al. (1978) relied on more traditional methods, such as counting the number of kicks. These findings indicate a need for systematic replications with modern techniques to gain a more nuanced understanding of motor learning across different age groups.

CRITIQUE ON MOBILE PARADIGM STUDIES

The most comprehensive criticism of the mobile paradigm is that unlike memory tasks (e.g., imitation task), it does not measure declarative memory (Bauer et al., 2007). This critique of Rovee-Collier and colleagues has endured from the early years of the mobile paradigm. Neuro-maturation accounts have argued that explicit/declarative memory is not yet fully formed during early infancy (Schacter and Moscovitch, 1984) and that the mobile paradigm only measures procedural/habitual memory Bauer (1996, 2004, 2007) and Bauer (2008) further argues that learning and memory measured with kicking behavior do not have any representational components and that infants' actions in the mobile paradigm might rely on brain structures, such as the cerebellum, which mature quite rapidly in the early stages of development.

Other criticism has focused more on methodological challenges. The mobile paradigm relies on cross-sectional data targeting specific age groups and is limited to group-level analysis. As a result, individual differences in learning and memory performance of infants are mostly ignored. For example, a meta-analysis conducted with mobile paradigm studies showed that 15% of the infants were excluded from the analysis because they did not learn the task (Gerhardstein et al., 2012). In some cases, the infants who did not satisfy the learning criteria constituted 25% (Gerhardstein et al., 1998; Hildreth et al., 2003), 30% (Gulya et al., 1998; Hildreth et al., 2003; Cuevas et al., 2015), 44% (Sweeney and Rovee-Collier, 2001) and even 50% of the sample (Tripathi et al., 2019). According to the learning criteria, infants were expected to exceed 1.5 times their baseline movement rate at any two consecutive minutes of the acquisition phase (Rovee-Collier et al., 1985; Hayne et al., 1986). This definition focuses on operant conditioning where the movement of the mobile functions as the reinforcer (Rovee and Rovee, 1969; Fagen et al., 1976). However, this approach can only draw a very limited picture of learning and memory in the mobile paradigm for two reasons. First, it discounts situations where infants use different learning strategies, especially the ones that can cause nonlinear behavior. Second, if the sample consists of only infants who can learn the task, in other words, the ones who satisfy the learning criteria, then the conclusions are limited to the behavior of those who were able to satisfy the criteria for operant conditioning. Thus, it remains unknown to what extent these findings are generalizable and what infants actually know and can learn.

A recent critique of the replicability of this learning effect by Jacquey et al. (2020a) pointed to the publication failures of several research groups due to unreliable learning effects. They noted that learning and memory of infants in the mobile paradigm were inferred from observational techniques (e.g., counting the number of kicks), with an imprecise operational definition of kicking behavior. For instance, recent pilot work in our lab with the traditional mobile setup showed that infants performed actions different than kicking (e.g., small foot movements when the leg is in an extended position) to activate the mobile. Second, control groups were presented with the stimulus manually, in a way that the experimenter moves the mobile at a particular rate (Rovee and Rovee, 1969; McKirdy and Rovee, 1978; Rovee-Collier et al., 1978) which might have resulted in unintended biases in implementing the experimental procedure. These control studies were the first ones testing and supporting the claim that infant learning during the mobile paradigm was a result of the contingency rather than caused by other factors such as excitement, visual or haptic stimulation. However, this assumption has not been tested with technological tools that allow in-depth analysis of movement characteristics and controlling for other variables that could lead to movement increase such as haptic feedback on the limbs.

The two most commonly used memory measures in the mobile paradigm (baseline and retention ratio) have been criticized for overestimating the strength of the retention (Bogartz, 1996) which put the reliability of these measures into question. Bogartz (1996) argued that even when memory strength is zero (e.g., when forgetting is complete), it is mathematically implausible for the retention ratio to be zero because the value (e.g., kicking rate) in long term retention test divided by another value in immediate retention test will be more than zero. Moreover, retention tests that are introduced right after the learning takes place (e.g., immediate retention test) usually facilitate memory consolidation and the strength of the memory. Retention ratio relying on the outcome of immediate retention test would be contaminated by this consolidation process, thus overestimating the memory strength.

It is also worth noting that the literature on the mobile paradigm has often involved Rovee-Collier and her collaborators both during her time and after her death in 2014 (Vitello, 2014). Replications from within the same research group are more likely to result in replication success than from other research groups because researchers within Rovee-Collier's group might be more hesitant about publishing results that are contradictory to their previous findings (Ioannidis, 2005; Makel et al., 2012). Thus, there is a need for both exact and conceptual replications by other scientific teams. Furthermore, replication of the key findings in the mobile paradigm literature with new behavioral, neural, and computational methods and advanced analysis techniques seems to be crucial for evaluating previous findings and developing new protocols.

In addition to methodological issues, we would like to bring up an additional point of critique that is not raised in the literature so far. The sensorimotor aspect of the mobile paradigm is mostly neglected and results have often been interpreted as a sign of perceptual and memory processes of young infants (Rovee-Collier and Sullivan, 1980; Rovee-Collier et al., 1981; Fagen and Rovee-Collier, 1983; Suss et al., 2012; Merz et al., 2017; Tripathi et al., 2019). Motor behavior was even considered a substitute for verbal behavior. Rovee-Collier (1997, p. 471) stated that "Infants "tell" us whether or not they recognize the test mobile [. . .]. If infants recognize the test mobile, then they say "yes" by kicking at a rate higher than their individual baseline rates; if they do not recognize the test mobile, then they say "no" by not kicking above their baseline rates." The fact that the mobile paradigm was not associated with its sensorimotor nature is paradoxical not only because sensorimotor learning is the backbone of the paradigm, but also because the outcome variable is a kinematic measure (e.g., number of kicks). The key problem with this view is that it creates a gap between knowledge representations acquired through high order cognitive processes (e.g., perceptual learning, declarative memory, category learning), sensorimotor experience, sensorimotor memories, and procedural learning. Furthermore, it overlooks the importance of the infant's dynamic relationship with the world in the early stages of development (Piaget, 1952; Thelen et al., 2001; Thelen, 2005). The lack of emphasis on sensorimotor experience in the work by Rovee-Collier and colleagues might be considered the product of the research zeitgeist of the time. It is in line with classical accounts of cognition which assert that motor behavior is only a medium to form amodal knowledge representations (Fodor, 1983).

NEW EMBODIED ACCOUNT ON MOBILE PARADIGM

The last two decades have seen a growing trend towards embodied accounts of cognition and development. It has been argued that knowledge representations are modal and dependent on action and perception (Niedenthal et al., 2005; Barsalou, 2010). Moreover, the role of motor experience (Von Hofsten, 2004; Sommerville et al., 2005; van Elk et al., 2008) and embodiment (Thelen et al., 2001; Smith, 2005; Westermann et al., 2007; Gredebäck and Falck-Ytter, 2015; Gottwald et al., 2016; Corbetta et al., 2018) on cognitive development has received a lot of attention. Together, these perspectives claim that the body is not only a tool to understand the higher-order cognitive processes but it is a crucial aspect of the infant's dynamic sensory interaction with the world. We propose a new embodied account of the mobile paradigm which shifts the spotlight from classical accounts of cognition to an understanding that puts the infant's active exploration and ability to detect sensorimotor contingencies at the center. This new account aims to take the mobile paradigm out of its confined and dis-embodied context and place it in a broader one, which takes sensorimotor experience and variability into consideration while arguing for new mechanistic explanations.

The new embodied account draws support from other studies in the field of infancy research arguing that the contingent relationship between body and environment forms the basis of learning in the very first months of life. When newborn infants direct their arm movements towards a light source this is done to facilitate the coupling between proprioceptive feedback and visual information (van der Meer et al., 1995; van der Meer, 1997). This visuomotor coupling produced by contingencies between self-initiated movements and environmental feedback has been proposed to constitute the emergence of reaching (Corbetta et al., 2014). Similarly, when learning the correspondences between the body and immediate environment, facilitates the development of body representations (Thomas et al., 2015; Hoffmann et al., 2017). While arm-based learning is more prominent at the beginning of life (Rochat, 1993), caudal body parts (e.g., hips, legs) are integrated into infants' body representation as infants gain more experience with leg-based learning (Watanabe and Taga, 2011; Thomas et al., 2015). Recently, studies focusing on the ability to learn contingencies revealed that detecting the contingency between a specific limb movement and mobile is an ability that develops with age (Watanabe and Taga, 2006; Jacquey et al., 2020b). Development involves an ever-changing process of interaction between perception and action. Measuring exactly the capacity for such integration, the mobile paradigm offers an opportunity to understand how learning sensorimotor contingencies unfold in real-time.

Pioneering work on the dynamic systems theory of development has made it evident that interaction of multiple factors (e.g., physical characteristics of infant, environment) and variability are crucial aspects for the emergence of new behavior (Thelen, 1995; Smith and Thelen, 2003). For instance, submerging an infant's legs in the water results in more stepping behavior whereas increasing the weight of the body leads to less kicking at 6 weeks of age, suggesting that even a minor change could impact the system considerably (Thelen et al., 2002). Furthermore, the variability in performed actions increases before a particular motor behavior is learned (Thelen, 1979). The work done by Rovee-Collier and colleagues never goes beyond the group-level analysis while investigating the learning and memory processes of young infants. Contrary to this, we argue that the variance and multiple factors that affect the emergence of new motor behavior are keys to unfolding the mobile paradigm and examining how young infants explore themselves and the world around them. Some studies in recent years have initiated the process of closing this gap in the literature. For example, it was emphasized that individual differences can be observed in the motor preferences of young infants while learning contingencies in the mobile paradigm (Thelen, 1994; Angulo-Kinzler and Horn, 2001; Watanabe and Taga, 2011).

It has been established that the visual system has two functionally distinct pathways in the cerebral cortex: the ventral pathway is for visual recognition and the dorsal pathway is for guiding action such as reaching for an object (Milner and Goodale, 1993, 2008). More recently, it is also acknowledged that these two streams continuously interact (Adamo and Ferber, 2009; Kitadono and Humphreys, 2009). The dorsal stream uses visual information for motor planning, guiding the body in space while executing motor behavior. Similarly, while infants in the mobile paradigm learn contingencies following visual and haptic feedback, they learn about their own bodies and affordances of their actions at the same time. Like learning any type of action, learned behavior in the mobile paradigm is retained over time and can be remembered in the presence of visual cues such as the room where the experiment took place or the linen draped over their cribs (Fagen and Rovee-Collier, 1983; Hayne et al., 1986; Butler and Rovee-Collier, 1989). The representation of learned actions decays over time (Rovee-Collier et al., 1981; Boller et al., 1990) and can be reestablished after a few trials when infants are reminded of learning context (Rovee-Collier et al., 1980; Fagen and Rovee-Collier, 1983; Muzzio and Rovee-Collier, 1996). Thus, both visual recognition capacity and guiding the action following the proprioceptive and visual feedback are important aspects of the mobile paradigm. We argue here that the dorsal stream may play a central role in learning sensorimotor contingencies in the mobile paradigm due to the similarity between functional properties of the dorsal stream and behavioral components of the mobile paradigm.

To sum up, we suggest an alternative view of the mobile paradigm which can be used for a more comprehensive analysis of motor behavior and related behavioral consequences. Instead of relying on the classical understanding of cognition, where actions are used to infer abstract and dis-embodied forms of symbolic cognition, we argue instead that sensorimotor experience, actions, and their variability should define the functional characteristics of the paradigm. Furthermore, we argue that this new description likely employs mechanisms that are responsible for guiding the action and body in space, as per the visual input. Recent literature both in developmental science in general and the mobile paradigm, in particular, is in line with this new embodied account and can be considered as an inevitable backlash against the traditional views which had overlooked the role of embodied experience in learning and memory. Concerning the interpretation of infant's behavior in the mobile paradigm, we provide a different interpretation than Rovee-Collier. We suggest that what has been measured all along is the ability to learn to act and interact, the development of a dorsally driven action memory, not the ability to represent and remember an abstract, adult-like manner.

CONCLUSIONS

Half a century ago, young infants' performance in the mobile paradigm started to challenge the accounts underestimating the learning and retention capabilities of infants in the first months of life. Recent findings using the mobile paradigm have opened up new discussions enabling in-depth analysis of the development of motor and cognitive skills through early infancy, more specifically by focusing on individual differences in learning sensorimotor contingencies. This review attempts not only to highlight the importance of the mobile paradigm in understanding cognitive and motor development of young infants but also to expose methodological and theoretical limitations of the literature which disregard the role of action and embodiment. Here, we proposed a new embodied account on the mobile paradigm that shifts the focus from what external behavior could reveal about the cognitive processes to an understanding of the development by incorporating action, representation, and variance.

AUTHOR CONTRIBUTIONS

US was responsible for writing the original draft, editing the manuscript, and visualization of graphs. GG was responsible for conceptualization, reviewing, and editing the manuscript. All authors contributed to the article and approved the submitted version.

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Movement Matters! Understanding the Developmental Trajectory of Embodied Planning

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Human motor skills are exceptional compared to other species, no less than their cognitive skills. In this perspective paper, we suggest that "movement matters!," implying that motor development is a crucial driving force of cognitive development, much more impactful than previously acknowledged. Thus, we argue that to fully understand and explain developmental changes, it is necessary to consider the interaction of motor and cognitive skills. We exemplify this argument by introducing the concept of "embodied planning," which takes an embodied cognition perspective on planning development throughout childhood. From this integrated, comprehensive framework, we present a novel climbing paradigm as the ideal testbed to explore the development of embodied planning in childhood and across the lifespan. Finally, we outline future research directions and discuss practical applications of the work on developmental embodied planning for robotics, sports, and education.

Keywords: embodied cognition, planning, lifespan, development, children

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1. INTRODUCTION

Humans start moving already in the womb, when they are just a few weeks old (Rahilly and Gardner, 1975), and develop the most sophisticated motor skills throughout the first years of life. Indeed, very young children are already able to thread a needle, build complex LEGO spaceships, and eat with chopsticks. Eventually, some humans reach a motor mastery that enables them to perform complicated heart surgeries or execute a triple twisting-double in gymnastics (the *Biles II*). Over the first years of childhood, humans' cognitive skills reach similar levels of extreme sophistication. Children can memorize entire poems, learn complex game rules, and manage to perform several tasks at the same time—eating, playing with a doll, binge-watching TV, and following a conversation simultaneously. Most adults can stay focused on the street and ignore irrelevant information while driving, and some are eventually able to control air traffic, play chess, and solve a Rubik's cube blindfolded. While newborns are far away from mastering any of these sophisticated motor or cognitive tasks, they will eventually acquire these or comparably complex skills throughout development. How do motor and cognitive development interact and impact each other? In this perspective paper, we argue that "movement matters!," implying that motor development is a crucial driving force of cognitive development, much more impactful than previously acknowledged. In this regard, we argue that to fully understand and explain developmental changes, it is necessary to consider the interaction of motor and cognitive skills from a developmental embodied cognition perspective.

In what follows, we first introduce developmental embodied cognition. Second, we exemplify our argument by introducing the concept of "embodied planning" integrating the motor and cognitive perspectives on planning and derive developmental predictions. Third, we present a novel climbing paradigm as the ideal testbed to capture and explore the development of embodied planning during childhood and across the lifespan. Finally, we outline future research directions and discuss practical applications of the work on developmental embodied cognition, and in particular of embodied planning, for robotics, sports, and education.

2. A DEVELOPMENTAL EMBODIED COGNITION PERSPECTIVE: WHY MOVEMENT MATTERS!

Hundreds of studies have documented the influence of sensorimotor manipulations on cognition, such as abstract spatial and temporal presentation (Loeffler et al., 2016), memory retrieval (Dijkstra et al., 2007), number processing (Fischer et al., 2004), or decision making (Lepora and Pezzulo, 2015). A central tenet of embodied cognition is that cognitive skills are "deeply routed" (Wilson, 2002) in the body, sensorimotor experiences, and the environment (Fischer and Coello, 2016). In this regard, it is already clear how crucial it is to consider the body as well as sensorimotor experiences and motor skills when trying to understand cognitive skills (Glenberg et al., 2013). From an embodied point of view, the interaction between sensorimotor and cognitive skills is theoretically predicted and has empirically been shown to be bidirectional and dynamic, although only a few studies have addressed the influence of cognition on sensorimotor processes (Engel et al., 2013).

Most sophisticated motor and cognitive skills are learned throughout development. Previous work already proposed that motor skills are the foundation of cognitive development (Ridler et al., 2006; Koziol et al., 2012; Gottwald et al., 2016) and provide the basis for learning (Adolph and Hoch, 2019). Different lines of research support this claim by showing that cognitive changes are associated with bodily changes (Hommel and Kibele, 2016), and that cognitive performance benefits from instructions activating bodily experience through body analogies (Pouw et al., 2016) or from acting (Lozada and Carro, 2016). Gottwald et al. (2016) recently demonstrated an association between motor control and executive functions in infants, finding that prospective motor control during reaching (i.e., peak velocity of the first movement) was correlated to inhibition and working memory. The potential magnitude of the impact of early motor skills on cognition is further demonstrated by a study from Ridler et al. (2006) showing that infants' gross motor skills predicted executive functions in adulthood. In particular, those infants who managed to stand and walk earlier in their life had superior cognitive skills in their thirties and showed higher gray-matter density in motor areas (Ridler et al., 2006).

There are several reasons why we argue that an *embodied cognition perspective* is extremely fruitful, if not necessary, to understand the developmental trajectory of motor–cognitive interactions. Together, bodily growth and the acquisition of new motor skills enable and support children's learning, acting as a driving force of cognitive development (Adolph and Hoch, 2019). Across the lifespan, human experience consists of an alternation of phases characterized by rapid change and phases of greater stability. In phases of change, embodiment effects can be captured particularly well: When our bodies change more dramatically and motor skills improve notably, as during infancy, childhood, and adolescence (Portella et al., 2017; Adolph and Hoch, 2019), or in older age (Cole et al., 2019), the impact of these changes on cognitive processes can be more easily scrutinized, and a time-ordered, causal direction can be tested.

In this perspective paper, we support this claim by focusing on the development of planning throughout childhood. Developmental research on motor and cognitive planning exists unnoticed from each other. However, we argue that both motor and cognitive components need to be considered jointly to understand the developmental trajectory of planning and its relevance for actions in the real world, beyond controlled lab environments.

3. EMBODIED PLANNING: INTEGRATING THEORETICAL AND METHODOLOGICAL APPROACHES

3.1. Motor Planning

Motor planning is defined as the ability to organize motor behavior to accomplish an anticipated goal-directed action. By definition motor planning processes depend on goal proximity: To adjust motor behavior to an imminent goal is referred to as first-order motor planning, whereas adjusting to subsequent goals is referred to as second-order motor planning (Rosenbaum et al., 2012; Domellöf et al., 2020). In tasks assessing motor planning, participants are required to first plan and then execute a motor sequence, during which the motor system needs to be controlled and can be adjusted. Classic motor planning tasks, used with children as well as with adults, are the bar-transport task (Knudsen et al., 2012), the overturned-glass task (Adalbjornsson et al., 2008; Knudsen et al., 2012), and the handle rotation task (Craje et al., 2010). In the bar-transportation task, for example, children are asked to insert a bar into a small opening of a box. In the trials requiring two-steps planning, children need to grasp the bar with a (rather uncomfortable) thumb-down grip, then rotate the bar by 180 and conclude the insertion in the much more comfortable thumb-up position. Second-order motor planning is somewhat limited until the age of 6 years (Benson et al., 2018), although improvements between the age of 3–6 years have been reported (Knudsen et al., 2012). At the age of 10, children usually reach adult-like motor planning skills (Benson et al., 2018).

3.2. Cognitive Planning

Cognitive planning is defined as the ability to think about action sequences in advance, thus approaching a task in an organized, strategic, and efficient manner (Anderson, 2002; Best et al., 2009), and is considered an essential requirement of goal-directed behavior. In tasks assessing cognitive planning, participants are required to plan ahead, evaluate, implement, and then potentially modify a sequence of actions (Best et al., 2009). Classic cognitive planning tasks used across the lifespan are the Tower of London (Bull et al., 2004) or maze navigation tasks (Völter and Call, 2014), where children are asked to move a reward through multiple levels of a maze. For planning which route to take, children have to consider whether the passages on the next levels are open or closed. Being a higher-order cognitive function that relies on working memory and inhibition (Best and Miller, 2010; McCormack and Atance, 2011), cognitive planning skills emerge rather late. For instance, 4-year-olds can plan only one step ahead, that is, considering only the configuration of passages onto the immediate next level of the maze, whereas 5-year-olds can plan two steps ahead (Völter and Call, 2014). Planning complex action sequences develops in late childhood or adolescence (Best et al., 2009), and only by the age of 15 children reach adult-like cognitive planning skills (Huizinga et al., 2006). Besides, even adults do not always plan as efficiently as possible (Meder et al., 2019).

3.3. Theoretical Integration of Motor and Cognitive Planning

The developmental trajectories of motor and cognitive planning have been studied separately. However, the interaction of motor and cognitive planning in general, and in particular during development, is to date not well understood. Specifically, cognitive planning has largely been investigated with tasks entailing no (or to a very low degree) motor planning or ignoring the motor component altogether. In this paper, we introduce the concept of "embodied planning," which integrates perspectives and methods from cognitive and movement sciences.

Embodied planning involves cognitive planning, which takes place before starting the execution of a motor-cognitive task, but assumes that one's bodily state, physical constraints, and (previous) motor experience provide cues for the planning process (cf. similar models in choice: embodied choices; Cisek and Pastor-Bernier, 2014; Wyer, 2016; Raab, 2017). Therefore, cognitive planning is *guided* by the awareness of how exactly a step can be executed through coordination of the motor systems (Raab et al., 2005), and by the feedback from the motor implementation at any previous step. Accordingly, embodied planning can be conceptualized as a dynamic, continuous feedback-loop between motor and cognitive planning in a goal-directed planning task, as illustrated in **Figure 1**.

3.4. Developmental Predictions

Based on the theoretical notion of embodied planning and the existing developmental evidence reviewed above, we can derive predictions at different levels of specificity. In general, we expect that the development of embodied planning across childhood will follow a nonlinear trajectory (Best et al., 2009), depicting stronger changes during infancy, early childhood, and adolescence—phases of more pronounced bodily change. More specifically, we predict that bodily changes will affect the motor aspects of planning first, the improvement of which will promote cognitive planning. Previous developmental findings support this claimed chronology, showing that although the motor planning skills reach maturity already around 10 years of age, cognitive planning develops way beyond age 10, reaching adult-like sophistication only in late adolescence. This developmental chronology might suggest that, indeed, cognitive planning skills are preceded by, fostered by, and build on improved motor planning skills.

Zooming in on this proposed developmental trajectory of embodied planning right on the onset of bodily change, we would predict that bodily changes first entail learning new motor skills and adapting already acquired ones, which in turn would trigger changes in motor planning. Changes in motor planning might then impact cognitive planning performance negatively, taking away additional resources required to fulfill the new motor planning demands (cf., embodied-cognitive-load hypothesis Warburton et al., 2013; for a summary of developmental work, see Berger, 2010; Berger et al., 2018). However, once the new motor skills are mastered and the corresponding improvements in motor planning are assimilated, cognitive planning might also improve, benefiting from motor planning efficiency.

3.5. Methodological and Technological Advances

The integrative theoretical approach and developmental predictions we propose have important methodological consequences. To be able to empirically capture and study the developmental trajectory of embodied planning, new designs, tasks, and measures have to be developed and implemented.

First, experimental *designs* should allow monitoring intra-individual changes and inter-individual differences throughout development. Intra-individual changes can be tested in longitudinal designs (Musculus et al., 2019), as well as in intervention and training studies (Harbourne and Berger, 2019). Inter-individual differences can be analyzed with cross-sectional comparisons of different age groups (Berger et al., 2015; Benson et al., 2018). Ideally, longitudinal, intervention, or training designs should be combined with cross-sectional age-group comparisons to best disentangle the developmental dynamics from individual differences and control for potentially confounding variables.

Second, the planning *tasks* should exert similar demands on both the motor and the cognitive systems, that is, both motor and cognitive planning skills should be required to solve the task, and to a similar extent. Additionally, the movements executed for and/or during the task need to be *task relevant* (Wilson and Golonka, 2013), not simply constituting a random motor response (pressing a button) that could be potentially interchanged with any other simple motor reaction (pulling a lever). Third, the *measures* implemented should be able to capture motor and cognitive interactions in embodied planning, ideally online. This is why we propose to combine movement analysis with reaction times. In developmental research, movement analysis has been proven an objective, fine-grained method to assess motor development (van Schaik and Dominici, 2020). In particular, marker-based motion tracking systems can provide accurate measures of motor processes

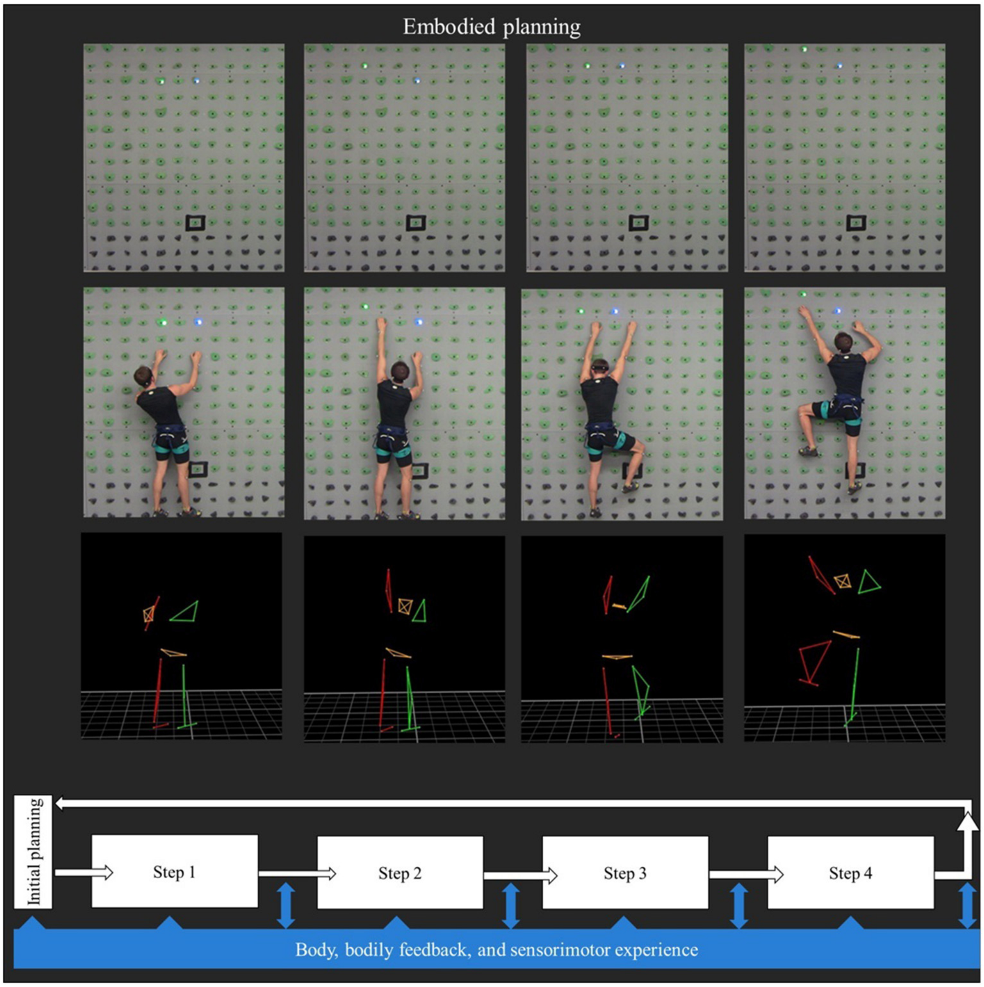

FIGURE 1 | Embodied planning in a climbing paradigm. The figure depicts four steps of embodied planning during a goal-directed climbing task. At the bottom, the embodied-planning concept is modeled as a dynamic, continuous feedback-loop between motor and cognitive planning. The two upper panels show an interactive climbing wall (2.40–3.60 m) with touch-sensitive climbing holds, which can light up in different colors and capture reaction times (i.e., ClimbLing system). The climbing system is synchronized to a movement-analysis system (Vicon; 10 infrared cameras at 119.88 Hz, VICONTM, Oxford, UK), which captures full-body movement kinematics as indicated by the stick figure of the body.

(van Schaik and Dominici, 2020). With marker-based systems, the position of children's joints can be tracked with specific camera systems while they move. During task execution, movement trajectories in 3D space can be captured (i.e., kinematics, see **Figure 1**). Although developmental studies exist that analyzed children's kinematics and response times (Domellöf et al., 2020), only a few combined the measures to explore the interaction between motor and cognitive skills (for an exception, see Gottwald et al., 2016). Domellöf et al. (2020) analyzed age-related differences in the spatiotemporal segmentation of the movement path for the wrist, index finger, and object during a peg fitting task. Their kinematic analyses provided a more detailed picture of the time course of motor planning and revealed developmental differences: While adults rotated the peg during transport, 6–10 year-old children most often did so only after reaching the goal. Integrating kinematics to the previously used cognitive measures allowed to capture that children did not engage in planning ahead as much as adults did, thus demonstrating less efficient motor planning. Along the same lines, the work of Gottwald et al. (2016) revealed that the peak velocity of infants' first movement in a prospective planning task captured the extent of their motor planning, which was related to their higher-order cognitive control. These studies highlight how the combined analysis of motor and cognitive processes is necessary to capture embodied-planning development in childhood.

To exemplify the design, task, and measurement requirements presented, we introduce a novel climbing paradigm to capture the developmental dynamics of embodied planning accordingly.

4. CLIMBING AS A TESTBED FOR EMBODIED PLANNING

Climbing to a predefined goal naturally involves embodied planning, requiring both complex cognitive (Cascone et al., 2013) and motor planning (Testa et al., 2003) skills. To successfully climb, one needs to plan *which* route to climb—which holds to use, and in what order—as well as *how* to execute the route (Raab, 2017). In particular, climbers need to consider their body constraints and the motor skills required to execute every single move. Then, during climbing, continuous sensorimotor (e.g., of muscles, hands, feet) and cognitive (e.g., which hold should I use next?) feedback fuels back, dynamically, into the ongoing planning process.

Crucially, climbing tasks are perfectly suitable to be used with a very wide age range, as they can be performed (and with great fun) by young children and adults (Croft et al., 2018). Indeed, children have a natural tendency to climb all sorts of things, from home furniture to playground constructions, to trees. Further, experimental climbing tasks can be used to explore body and action boundaries (van Knobelsdorff et al., 2020; Seifert et al., 2021), also in children (Croft et al., 2018): A recent study showed that 6- to 11-year-old children who were more accurate in judging their reaching capability (i.e., whether they were able to reach and grasp holds that are near or far away) completed more climbing routes successfully and did so faster (Croft et al., 2018).

Methodologically speaking, goal-directed climbing comprises motor and cognitive planning before the task and during execution. In experimental settings, climbing tasks can be easily adjusted and modified to manipulate cognitive and motor demands, such that motor planning but only little cognitive planning is required, or the other way around. In particular, cognitive planning could be minimized by guiding children through all steps (i.e., hold) along a predefined route. In particular, by using an interactive climbing wall (e.g., ClimbLing), one could indicate the next hold that children should use by lighting it up. To reduce cognitive planning to a minimum, the next hold would light up only after the previous hold has been touched (please refer to **Figure 1**). At the same time, motor planning could be reduced to a minimum by asking children to plan a route without executing it. In particular, children could be asked to plan a climbing route by just indicating to the experimenter which holds they would use using a laser pointer or on an app that displays the climbing wall. Thus, by carefully designing novel climbing tasks, motor and cognitive planning processes could be disentangled experimentally.

Given in regular climbing motor and cognitive planning constantly interact, the joint consideration of motor and cognitive measures in climbing experiments is warranted. From the motor side, anthropometric measures and movement analyses associated with climbing performance should be captured, such as weight (Mermier et al., 2000; Watts et al., 2003), height (Watts et al., 2003; Laffaye et al., 2016), body mass index (Laffaye et al., 2016), grip strength (Mermier et al., 2000), finger-tip strength (van Knobelsdorff et al., 2020), and Ape-index (Mitchell et al., 2011). For movement kinematics, spatial and temporal movement dimensions should be considered (Orth et al., 2016, 2017). In particular, the immobility–mobility ratio (IMR) and the geometric index of entropy (GIE) represent temporal-spatial indices capturing motor planning in climbing (Orth et al., 2017). Importantly, the movement data should be time-matched and related to cognitive measures during the task, such as the number of holds to indicate planning steps (Huizinga et al., 2006), the time used to complete the route, and the initial planning time used before starting task execution (Huizinga et al., 2006). Complementing these "classical" cognitive planning variables by capturing gaze patterns during initial route preparation (Seifert et al., 2017; van Knobelsdorff et al., 2020) and the time course of movement variability during route execution can provide a better picture of the planning strategies.

Together, due to the close connection of motor and cognitive planning during goal-directed climbing, the ongoing embodied-planning dynamics can be captured and the performance in previous planning steps can be related to the next and so forth. Climbing as a task is useful because completing a route is only possible by a sequence of embodied-planning steps. Therefore, the unfolding of motor and cognitive processes from initially planning a route through route execution can shed light on the interaction—embodied planning.

5. FUTURE RESEARCH DIRECTIONS AND POTENTIAL APPLICATIONS OF EMBODIED PLANNING

Improvements in embodied planning across the lifespan can be seen as a goal on its own, or as a means to an end. On the one hand, research on embodied planning can support coaches and teachers in developing interventions that target and boost motor planning skills during the school-age years (Croft et al., 2018), e.g., by introducing climbing exercises as an integral part of PE curricula. On the other hand, embodied planning could also serve as a means to improve sports and academic performance. Recent results indicate that executive-function training through sports in school has positive effects with near transfer (Vazou et al., 2016). Embodied-planning training might be especially beneficial for students with lower academic skills (Pouw et al., 2016) or children with developmental delay (Harbourne and Berger, 2019). Indeed, children with a lower level of general mathematical abilities performed better in a physical problem-solving task when the instructions provided references to their bodies, for example when children had to mimic a lever with their arms (Pouw et al., 2016). Also children with developmental delays profited from a motor-based problem-solving intervention in terms of motor and cognitive gains (Harbourne and Berger, 2019). Thus, making use of the body, activating bodily representation, and providing (active) sensorimotor experience during embodied-planning exercises might constitute a promising intervention in sports and education.

Broadening the scope, we believe that experimental research on embodied planning could inform the development of more accurate and sophisticated models of human movement to be implemented in developmental robotics. First, fueling children's kinematics into a robotic system would support the development of robots able to move and plan *adaptively*. Second, developmental, cognitive, and movement scientists can profit from the robotic implementation of embodied-planning research to better understand developmental trajectories and individual differences in motor and cognitive development, and their interaction. Researchers could use simulations to test whether the way a person planned and executed their movements was functional or not. Along these lines, Ossmy et al. (2018) trained soccer-playing robots with kinematic walking data generated by infants during free play. The robots trained with a high variance of kinematic patterns won the simulated season of "RoboCup" (Ossmy et al., 2018) against robots trained with a low variance of kinematics. Similarly, aspects of motor planning in climbing such as the IMR or GIE could be evaluated. In detail, the kinematics of children climbing and of adults climbing can be fed into a robotics simulation. In the next step, the respective efficiency can be modeled, and, based on this, climbing training could be designed aiming at specific, efficient movement patterns.

6. CONCLUSION

In this perspective paper, we adopted a developmental embodied cognition perspective to argue that "movement matters!" for understanding the emergence and developmental trajectory of motor and cognitive skills, as cognitive development is fundamentally driven and constrained by motor development. We supported this claim by reviewing recent literature on motor and cognitive planning, so far researched in isolation. We then introduced the integrative theoretical concept of "embodied planning," together with a novel climbing paradigm and related measures allowing to test it. Thereby, we intend to bridge the gap between the motor and cognitive disciplines. Overall, we highlighted the added value of embodied-planning research: Playful embodied-planning interventions could promote children's learning in the school setting and beyond. In the long run, embodied-planning research could contribute to the development of a new generation of adaptive robots.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

LM drafted the article, which was edited by and discussed with AR and MR. All authors contributed to the development of this perspective and agree to be accountable for the content of the work.

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Regenerative Virtual Therapy: The Use of Multisensory Technologies and Mindful Attention for Updating the Altered Representations of the Bodily Self

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The term "regenerative medicine" (RM) indicates an emerging trend in biomedical sciences that aims at replacing, engineering, or regenerating human cells, tissues, or organs to restore or establish normal function. So far, the focus of RM has been the physical body. Neuroscience, however, is now suggesting that mental disorders can be broadly characterized by a dysfunction in the way the brain computes and integrates the representations of the inner and outer body across time [bodily self-consciousness (BSC)]. In this perspective, we proposed a new kind of clinical intervention, i.e., "Regenerative Virtual Therapy" (RVT), which integrates knowledge from different disciplines, from neuroscience to computational psychiatry, to regenerate a distorted or faulty BSC. The main goal of RVT was to use technology-based somatic modification techniques to restructure the maladaptive bodily representations behind a pathological condition. Specifically, starting from a Bayesian model of our BSC (i.e., body matrix), we suggested the use of mindful attention, cognitive reappraisal, and brain stimulation techniques merged with high-rewarding and novel synthetic multisensory bodily experience (i.e., a virtual reality full-body illusion in sync with a low predictability interoceptive modulation) to rewrite a faulty experience of the body and to regenerate the wellbeing of an individual. The use of RVT will also offer an unprecedented experimental overview of the dynamics of our bodily representations, allowing the reverse-engineering of their functioning for hacking them using advanced technologies.

Keywords: embodiment (and its derivatives), multisensory integration, Bayesian surprise maximization, bodily full-body illusions, brain stimulation, interoceptive technology, virtual reality, mindfulness

INTRODUCTION

Holmes et al. (2014) published, in Nature, the article "Psychological treatments: A call for mental-health science," calling for an alliance between clinicians and neuroscientists to advance our understanding of psychological treatments. They underlined that "we do not yet fully understand how psychological therapies work—or when they don't. Neuroscience is shedding light on how

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Abbreviations: AR, autobiographical recall; BSC, bodily self-consciousness; GVS, galvanic vestibular stimulation; PAF, positive affective forecasting; RCT, randomized controlled trial; RVT, regenerative virtual therapy; tDCS, transcranial direct current stimulation; TMS, transcranial magnetic stimulation; VNS, vagus nerve stimulation.

to modulate emotion and memory, habit, and fear learning. But psychological understanding and treatments have, as yet, profited much too little from such developments." (p. 288) A key problem underlying most, if not all, psychopathologies is schema rigidity (Morris and Mansell, 2018): many individuals are unable to avoid and update automatic beliefs and behaviors that rely on preexisting or underlying assumptions and evaluations that might not apply to the current situation with significant negative effects.

However, recent key discoveries in neuroscience are outlining a new conceptual framework, merging the embodied cognition approach (Clark, 2016b; Newen, 2018) with the predictive brain hypothesis (Friston, 2010; Owens et al., 2018), on how self-schemas influence the psychological functioning that directly links them to the processing of multisensory bodily signals (Blanke et al., 2015; Riva, 2018). Paulus et al. (2019) recently explained that "these conceptual models suggest that mental disorders can be broadly characterized by a dysfunction in the way the brain computes and integrates representations of the inner and outer worlds of the body across time. According to this view, changes in mood and anxiety are a by-product of the brain's biased translation of what it expects will happen versus what is actually happening in these worlds, producing a persistent discrepancy/error signal when outcomes are observed." (p. 99).

Following this vision, in the last decade, several mental health conditions have been associated with damage and/or malfunctioning of the bodily self, i.e., eating and weight disorders (Riva and Gaudio, 2012; Keizer et al., 2013; Dakanalis et al., 2016; Scarpina et al., 2016; Riva and Dakanalis, 2018), depression (Barrett et al., 2016), schizophrenia (Postmes et al., 2014; Klaver and Dijkerman, 2016; Ferri et al., 2017; Möller et al., 2021), autism (Ropar et al., 2018; Riva et al., 2019a), and chronic pain (Tsay et al., 2015; Di Lernia et al., 2016).

Nevertheless, since the study by Holmes et al. (2014), things have not changed significantly: these basic research discoveries have not yet met a direct clinical application. While the change mechanisms of successful psychotherapeutic approaches, such as the current gold standard for many mental diseases, i.e., cognitive behavioral therapy (CBT), are often based on schema modifications, they do not target directly with their methods all the components of a faulty bodily experience.

In 2014, the first author of this perspective suggested in a letter to Nature (Gaggioli and Riva, 2014) that the use of technology, and in particular virtual reality (Riva et al., 2019b), could be a possible solution to this problem, offering a powerful tool for improving evidence-based psychological treatments. More recently, the two different studies by Browning et al. (2020) and Nair et al. (2020) suggested the use of computational characterizations/assays of behavior for patients undergoing psychological therapies using mathematical/Bayesian models of key cognitive processes.

In this perspective, we wanted to follow both suggestions by introducing a new therapeutical approach, i.e., Regenerative Virtual Therapy (RVT). Specifically, starting from a Bayesian model of our bodily self (i.e., body matrix), we suggested the use of mindful attention, cognitive reappraisal, and brain stimulation techniques merged with high-rewarding and novel synthetic multisensory bodily experience to rewrite a faulty bodily experience and to regenerate the wellbeing of an individual.

FROM REGENERATIVE MEDICINE TO REGENERATIVE VIRTUAL THERAPY

In medicine, a profound paradigm shift was introduced by regenerative medicine (RM), an emerging trend in biomedical sciences that aims at "replacing, engineering, or regenerating human cells, tissues, or organs to restore or establish normal function" (Mason and Dunnill, 2008). The fundamental value of RM is the possibility to regenerate the organism and to force the body to heal itself. RM allows not only to better cope with the symptoms but also to eradicate the cause of the symptoms by helping the body to restore the damaged cells to a healthy state (Mason and Dunnill, 2008; Mahla, 2016).

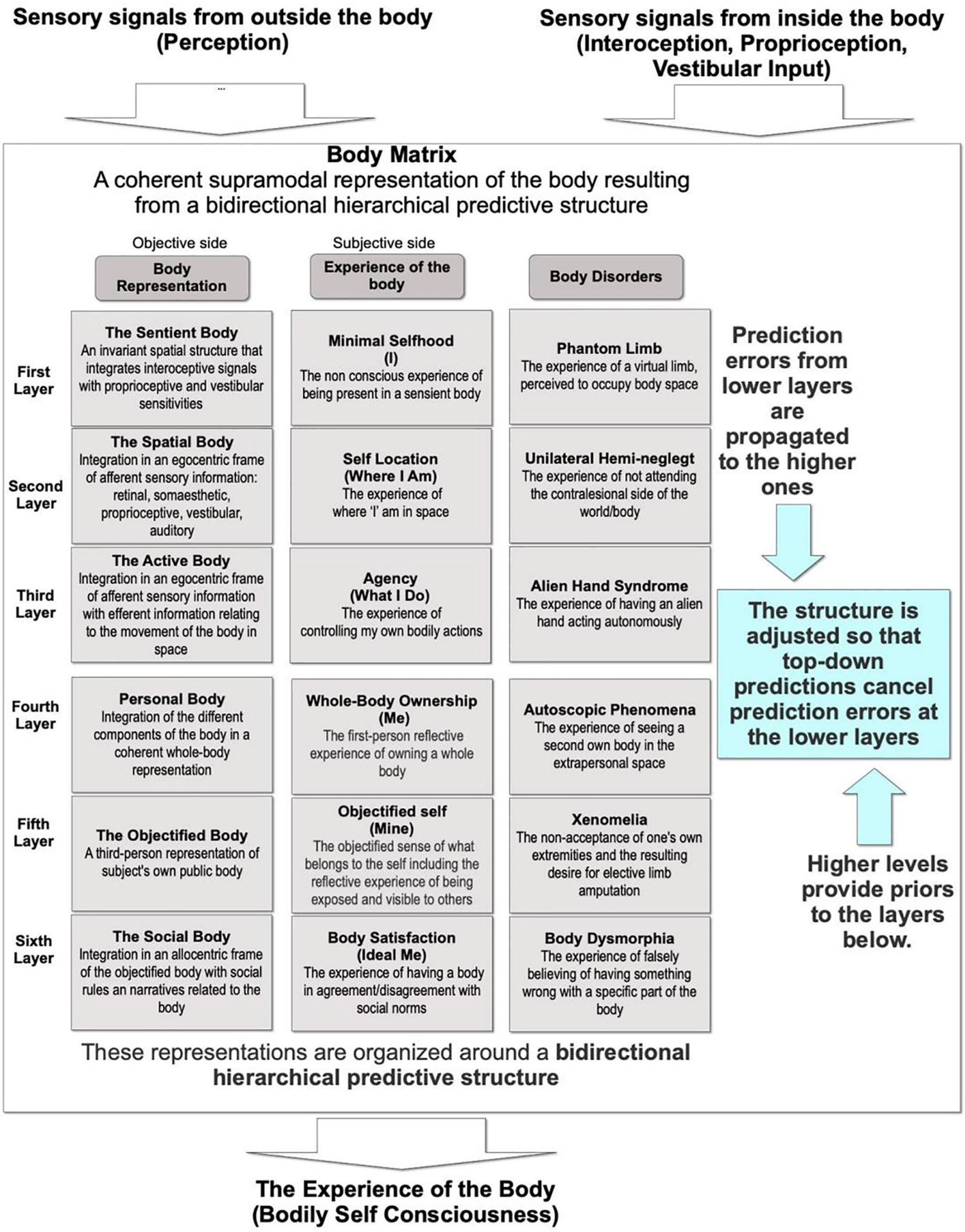
So far, the focus of RM has been the physical body: human stem cells and biomolecular therapies are used to restore the normal structure and function of a missing or damaged organ. However, the abovementioned evidence from recent neuroscientific discoveries suggests that by exploiting the mechanisms of the "predictive brain," it is also possible to regenerate our bodily experience [i.e., bodily self-consciousness (BSC)].

The BSC represents a challenging research field because it requires an interdisciplinary framework to provide a link between all the afferent levels and brain circuits involved in a particular bodily experience (Lux et al., 2021). However, recent neuroscience research (Blanke, 2012; Blanke et al., 2015; Riva, 2018; Park and Blanke, 2019) is shedding new light on the processes involved in the BSC.

Even if BSC is experienced by the individual as a unitary perception, neuroimaging and neurological data suggested that BSC includes different layers (**Figure 1**) that integrate both sensory and cognitive bodily data in a coherent experience (Moseley et al., 2012; Apps and Tsakiris, 2014; Riva, 2018).

Specifically, the layers are organized around a bidirectional hierarchical structure following the active inference and predictive coding paradigms introduced by the Bayesian brain theory (Apps and Tsakiris, 2014; Friston et al., 2014). The result of this process is a coarse supramodal multisensory representation of the body and the space around it (i.e., body matrix, refer to **Figure 1**), emerging from the flow of information across large-scale networks that link various regions of the brain (Moseley et al., 2012; Gallace and Spence, 2014; Sedda et al., 2016; Riva, 2018).

First, the Bayes' theorem (Manjaly and Iglesias, 2020) explains how an initial representation/layer (or "prior," a prediction based on a model of the environment and the body) is integrated with or updated by new observations (i.e., sensory input), resulting in an updated representation (or posterior probability). In this view, the possibility of updating a prior depends on the so-called prediction error, or "surprise" (Stephan et al., 2016): the discrepancy between new data and prior belief (i.e., predicted sensory information), which is weighted by the ratio



	Objective side Body Representation	Subjective side Experience of the body	Body Disorders
First Layer	**The Sentient Body** An invariant spatial structure that integrates interoceptive signals with proprioceptive and vestibular sensitivities	**Minimal Selfhood (I)** The non conscious experience of being present in a sensient body	**Phantom Limb** The experience of a virtual limb, perceived to occupy body space
Second Layer	**The Spatial Body** Integration in an egocentric frame of afferent sensory information: retinal, somaesthetic, proprioceptive, vestibular, auditory	**Self Location (Where I Am)** The experience of where 'I' am in space	**Unilateral Hemi-neglegt** The experience of not attending the contralesional side of the world/body
Third Layer	**The Active Body** Integration in an egocentric frame of afferent sensory information with efferent information relating to the movement of the body in space	**Agency (What I Do)** The experience of controlling my own bodily actions	**Alien Hand Syndrome** The experience of having an alien hand acting autonomously
Fourth Layer	**Personal Body** Integration of the different components of the body in a coherent whole-body representation	**Whole-Body Ownership (Me)** The first-person reflective experience of owning a whole body	**Autoscopic Phenomena** The experience of seeing a second own body in the extrapersonal space
Fifth Layer	**The Objectified Body** A third-person representation of subject's own public body	**Objectified self (Mine)** The objectified sense of what belongs to the self including the reflective experience of being exposed and visible to others	**Xenomelia** The non-acceptance of one's own extremities and the resulting desire for elective limb amputation
Sixth Layer	**The Social Body** Integration in an allocentric frame of the objectified body with social rules an narratives related to the body	**Body Satisfaction (Ideal Me)** The experience of having a body in agreement/disagreement with social norms	**Body Dysmorphia** The experience of falsely believing of having something wrong with a specific part of the body

FIGURE 1 | The body matrix.

between data precision (the confidence one assigns to the data) and prior representation precision (the confidence one assigns to a prior belief). In this view, when the precision of the data (i.e., likelihood) is higher than the precision of the prior representation, a large update results i.e., (the posterior moves more strongly toward the data Manjaly and Iglesias, 2020). Simply speaking, precise priors reduce, and precise sensory data increase the probability of a representation update.

Moreover, in a bidirectional hierarchical structure similar to the one used by BSC, higher levels provide priors to the level below, and these constraints are progressively tuned by the sensory input coming from the lower levels (Apps and Tsakiris, 2014; Clark, 2016a). Specifically, prediction errors are propagated to the higher level to adjust the structure of the model so that the top-down predictions cancel prediction errors at the lower level (Clark, 2016a). In this view, the greater is the prediction error at the bottom of the hierarchy (i.e., ascending prediction error), the further up the hierarchy its effects will percolate and lead to the adjustments of the model (Manjaly and Iglesias, 2020). In brief, the minimization of prediction errors involves a reciprocal exchange of signals between hierarchical levels: prediction errors ascend the hierarchy to revise expectations, which generate descending predictions that resolve or suppress prediction errors at the level below.

These principles and different recent studies suggest that it is possible to update the contents of our experience of the body both at a low level, i.e., proprioception and interoception (Henriques and Cressman, 2012; Nourouzpour et al., 2015; Di Lernia et al., 2018), and a high level, i.e., social cognition and self-identification (Tajadura-Jiménez and Tsakiris, 2014; Maister et al., 2015), using advanced technological tools. In the below sections, we further detailed the contents of our proposal: the use of technology-based somatic modification techniques to facilitate a potential revision of maladaptive predictions (priors). Specifically, we planned to use mindful attention, cognitive reappraisal, and brain stimulation techniques merged with high-rewarding and novel synthetic multisensory bodily experiences such as virtual reality bodily illusions.

REGENERATIVE VIRTUAL THERAPY TECHNOLOGY

Since the discovery of the rubber hand illusion (Botvinick and Cohen, 1998) and the emergence of non-invasive brain stimulation methodologies (Tatti et al., 2016), different researchers have used advanced technologies to alter body perceptions in clinical and non-clinical populations. In particular, three different approaches have been developed as follows:

1. **Virtual bodily illusions** (Matamala-Gomez et al., 2021), also known as full-body ownership illusions, use virtual reality technologies to trick the predictive coding mechanisms of the brain, thereby inducing users a sense of ownership over a virtual body.
2. **Interoceptive technologies** (Schoeller et al., 2019), modulate interoceptive signals. They include technologies for producing a direct modulation of interoceptive signals [i.e., c-fibers stimulation, Björnsdotter et al. (2010); Di Lernia et al. (2020); or sonoception, Wiederhold and Riva (2019)] and technologies generating illusions by providing false feedback of the physiological states of individuals (Iodice et al., 2019).
3. **Brain stimulation techniques**, for example, transcranial direct current stimulation (tDCS) and transcranial magnetic stimulation (TMS) (Avenanti et al., 2018; Mancuso et al., 2020; Stramba-Badiale et al., 2020), and also vagus nerve stimulation (Neuser et al., 2020) and galvanic vestibular stimulation (Ponzo et al., 2018, 2019) modify both bottom-up (Pollatos et al., 2016) and top-down (Marotta et al., 2021) bodily signals.

Existing studies, however, suggest that the effects of the abovementioned approaches on higher cognitive processes are temporary, even with non-pathological individuals. For example, as reported by Freeman et al. (2017), the longest follow-up in studies with virtual bodily illusions for correcting the perception of the body in participants with eating disorders is just 2 h (Keizer et al., 2016). In our opinion, this can be explained by the bidirectional hierarchical predictive structure used by BSC. In this structure, the minimization of prediction errors involves a reciprocal exchange of signals between hierarchical layers: prediction errors ascend the hierarchy to revise expectations, which generate descending predictions that resolve or suppress prediction errors at the level below. In this view, generating prediction errors in one layer is not enough to guarantee a revision on higher levels, producing the long-term modification of the BSC.

Following a prediction error, the contents of the body matrix are adjusted in evaluating the (dis)agreement between the perceived sensory activity, and the body experience predicted through the integration of contents from different bodily and cognitive representations (Talsma, 2015). Among others, three possible effects can be activated (Pezzulo et al., 2015; Owens et al., 2018; Mirza et al., 2019), namely, (1) prediction errors ascend the cortical hierarchy to change predictions (model updating), (2) predictions selectively sample sensory input to change the sensations being predicted to agree with their content (active inference) through action and/or attentional shifts, or (3) attention is used to optimize the precision afforded to different parts of the sensorium.

In general, prediction errors in a bidirectional hierarchical predictive structure generate a model updating only when:

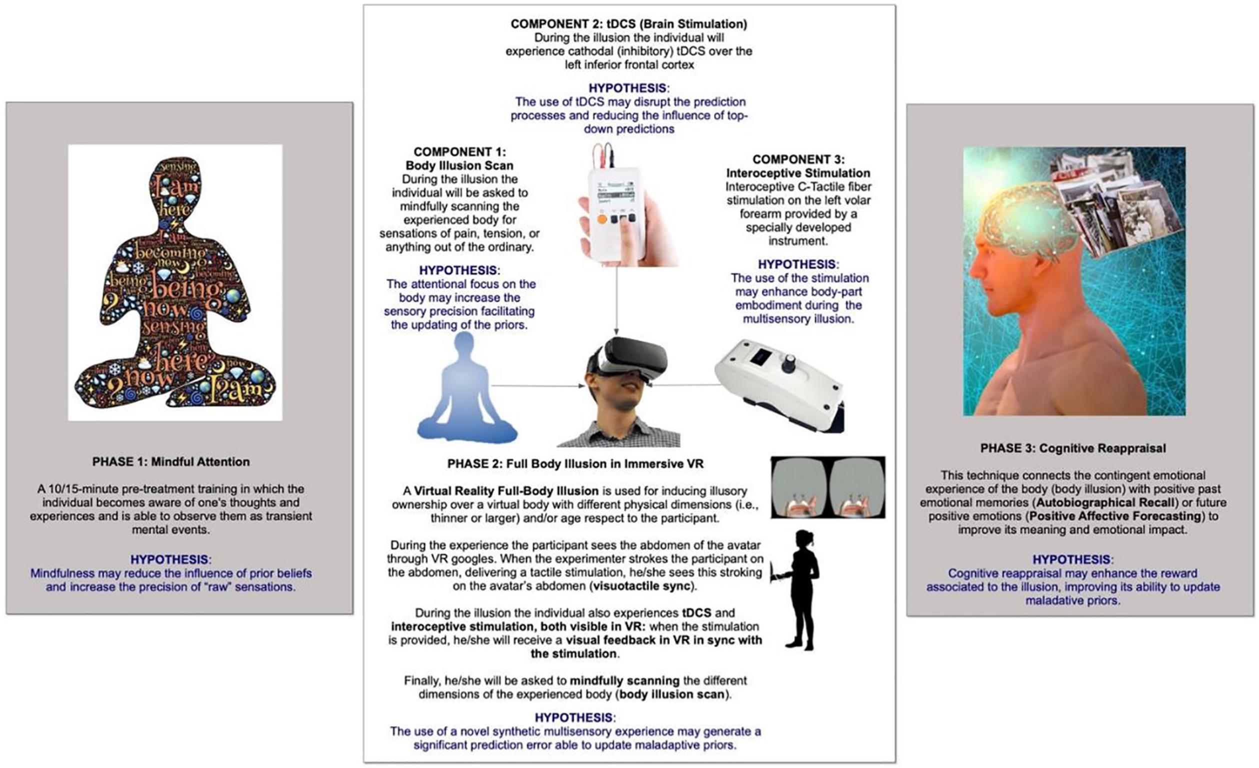
- **The extent of the prediction errors is high:** As we have noticed before, the greater is the prediction error, the further up the hierarchy its effects will percolate and lead to model adjustments (Manjaly and Iglesias, 2020). In general, prediction errors arise from the lower layers because they are easier to control and modify. However, errors can be generated in any of the layers of the body matrix (Clark, 2013).
- **The precision of the prediction errors is high:** During multisensory integration, bottom-up bodily signals from different sensory modalities and top-down predictions are weighted according to their contextual reliability and combined to produce a unitary experience of the body. This precision-weighting mechanism is critical for balancing appropriately prediction and sensory stimuli (Barca and Pezzulo, 2020): if it is wrong and it assigns to bottom-up sensory stimuli a low precision, the generated prediction error does not produce an update. Precision operates both within and between modalities, and it is improved both by the level of attention provided to the specific signal (Smout et al., 2019) and by reducing the noise of the sensory signal (Pezzulo et al., 2015).
- **The surprise of the prediction errors is high:** The results of a study by McGuire et al. (2014) suggest that the

level of surprise is related to three computationally and neuroanatomically distinct factors.

- The first one is the **extent of the prediction error.** The more the outcome is particularly unpredictable or surprising under the current model, the more is the probability of an update.
- The second one is **the relative uncertainty of the current model**. The higher is the level of uncertainty of the model, the higher is the probability of an update.
- The third one is the level of **reward**. The higher is the potential reward produced by the update, the higher is its probability. Possible rewards are a better image of the self or a positive emotional state.

In this view, the main goal of RVT was to allow a potential revision and de-weighting of maladaptive predictions through the integration of different technology-based somatic modification techniques with mindfulness and cognitive reappraisal. The suggested process is as follows (**Figure 2**):

1. **The development of a synthetic multisensory experience (visuotactile and interoceptive) able to generate significant prediction errors, for contrasting the dysfunctional internal model**: to reach this goal, we planned to use a virtual reality full-body illusion in a body different from the real one (i.e., an anorectic subject in a normal body) in sync with an interoceptive modulation. During the experience, when the experimenter strokes the participant on the abdomen, delivering a tactile stimulation, he/she observes this stroking on the abdomen of the avatar (visuotactile sync). The same happens during interoceptive stimulation: any stroke on the real hand is synched to the virtual one.
2. **The use of brain stimulation techniques to reduce the influence of top-down predictions**: to manipulate the process of precision-weighting, we suggested the use of tDCS to disrupt the prediction processes and to reduce the influence of top-down predictions. Avenanti et al. used both cathodal (inhibitory) and anodal (excitatory) tDCS over the left inferior frontal cortex, a key area of the action observation network involved in coupling action-perception with execution, during an action prediction task (Avenanti et al., 2018). Their results preliminarily suggest that down- and upregulating excitability using tDCS can hinder and enhance action prediction abilities, respectively.
3. **The use of mindfulness attention to improving the precision of the synthetic multisensory experience:** mindful attention (Papies et al., 2015) is defined as a form of attention that can increase the salience of the moment-by-moment experience and reduce the impact of predefined schemas. When mindfully attentive, people become aware of thoughts and experiences, observing them as transient mental events (Bennett et al., 2021).



PHASE 1: Mindful Attention

A 10/15-minute pre-treatment training in which the individual becomes aware of one's thoughts and experiences and is able to observe them as transient mental events.

HYPOTHESIS:
Mindfulness may reduce the influence of prior beliefs and increase the precision of "raw" sensations.

COMPONENT 2: tDCS (Brain Stimulation)
During the illusion the individual will experience cathodal (inhibitory) tDCS over the left inferior frontal cortex

HYPOTHESIS:
The use of tDCS may disrupt the prediction processes and reducing the influence of top-down predictions

COMPONENT 1:
Body Illusion Scan
During the illusion the individual will be asked to mindfully scanning the experienced body for sensations of pain, tension, or anything out of the ordinary.

HYPOTHESIS:
The attentional focus on the body may increase the sensory precision facilitating the updating of the priors.

COMPONENT 3:
Interoceptive Stimulation
Interoceptive C-Tactile fiber stimulation on the left volar forearm provided by a specially developed instrument.

HYPOTHESIS:
The use of the stimulation may enhance body-part embodiment during the multisensory illusion.

PHASE 2: Full Body Illusion in Immersive VR

A **Virtual Reality Full-Body Illusion** is used for inducing illusory ownership over a virtual body with different physical dimensions (i.e., thinner or larger) and/or age respect to the participant.

During the experience the participant sees the abdomen of the avatar through VR googles. When the experimenter strokes the participant on the abdomen, delivering a tactile stimulation, he/she sees this stroking on the avatar's abdomen (**visuotactile sync**).

During the illusion the individual also experiences **tDCS** and **interoceptive stimulation, both visible in VR:** when the stimulation is provided, he/she will receive a **visual feedback in VR in sync with the stimulation**.

Finally, he/she will be asked to **mindfully scanning** the different dimensions of the experienced body (**body illusion scan**).

HYPOTHESIS:
The use of a novel synthetic multisensory experience may generate a significant prediction error able to update maladaptive priors.

PHASE 3: Cognitive Reappraisal

This technique connects the contingent emotional experience of the body (body illusion) with positive past emotional memories (**Autobiographical Recall**) or future positive emotions (**Positive Affective Forecasting**) to improve its meaning and emotional impact.

HYPOTHESIS:
Cognitive reappraisal may enhance the reward associated to the illusion, improving its ability to update maladative priors.

FIGURE 2 | Regenerative virtual therapy.

Mindful attention is a primary component of mindfulness, which can be considered the awareness of being in the present moment without the burden of previous, mindless schemas (Pagnini and Philips, 2015). In Bayesian terms, this suggests that mindfulness may reduce the influence of prior beliefs and increase the precision of "raw" sensations (Manjaly and Iglesias, 2020). Preliminary findings supporting this hypothesis suggest that automatic reactions and behaviors (Papies et al., 2015), such as salivation following food conditioning (Baquedano et al., 2017), can be hindered with mindful attention.

4. **The use of cognitive reappraisal to reconstruct and re-elaborate the emotional content of the multisensory experience to improve its level of reward:** specifically, we planned to increase the level of reward by connecting the body illusion with positive past emotional memories [i.e., autobiographical recall (AR)] or future positive emotions [i.e., positive affective forecasting (PAF)] to improve its meaning and emotional impact. AR connects the contingent emotional experience of the body with past emotional memories of it (Robinson, 1986; Mills and D'Mello, 2014). Instead, PAF connects the body illusion to how the individual will feel in the future.

CONCLUSION

This perspective introduced the RVT, a new therapeutical approach that wants to address a critical feature of most, if not all, psychopathologies: schema rigidity (Morris and Mansell, 2018). According to a predictive brain neuroscientific approach, mental disorders can be broadly characterized by a dysfunction in the way the brain computes and integrates the representations of the inner and outer body across time (i.e., BSC). Specifically, inaccurate or inflexible predictions can disturb the coherent integration of bodily and visceral signals and disrupt the optimal interaction of an individual with the external and social world.

In this view, the main goal of RVT was to allow a potential revision and de-weighting of maladaptive predictions through the integration of different technology-based somatic modification techniques with mindfulness and cognitive reappraisal.

The perspective discussed the rationale of this approach and presented a specific strategy based on the following steps:

- The development of a synthetic multisensory experience (i.e., visuotactile and interoceptive) to generate significant prediction errors: a virtual reality full-body illusion in sync with an interoceptive modulation characterized by a low level of predictability.
- The use of brain stimulation techniques to reduce the influence of top-down predictions.
- The use of mindfulness attention to improving the precision of the multisensory experience.
- The use of cognitive reappraisal to reconstruct and re-elaborate the emotional content of the multisensory experience to improve its level of reward.

On the one hand, this framework is based on a clear rationale and allows the identification of different hypotheses (presented in **Figure 2**) that can be tested experimentally. On the other hand, the clinical testing of the different assumptions is not easy, not only experimentally but also technically and computationally. The biggest challenge is the complexity of the different multisensory bodily experiences to be developed that involve both internal and external signals and both somatic and semantic/metacognitive domains.

Moreover, the closed-loop nature of BSC means that a modification in one domain typically invokes a cascade of changes throughout the different layers, making it difficult to differentiate cause from consequence. This suggests that, on the one hand, it is complex to evaluate the effects of the treatment given the many variables involved. On the other hand, the regulation of bodily variables through homeostasis and allostasis makes particularly challenging to determine whether problems of a patient originate in inference problems, regulation problems, or actual bodily dyshomeostasis as these can all lead to one another (Petzschner et al., 2017).

Finally, the number of somatic perturbation techniques that can be used to generate prediction errors is actually limited to the ones described in the study. As underlined by Petzschner et al. (2017), developing new tools that are non-invasive and provide temporal control is critical for the future of RVT. Moreover, the increasing availability of tools that allow the acquisition and (computational) analysis of neuroimaging and behavioral data may facilitate the validation of the model (Frässle et al., 2021).

In conclusion, RVT offers an empirically testable and potentially clinically useful framework that can improve the existing state-of-the-art in different ground-breaking ways, allowing us as follows:

- to acquire an unprecedented experimental overview of the dynamics of our bodily representations.
- to explain how somatic processes affect mental health and wellbeing.
- to reverse-engineer their functioning and hacking them using interoceptive and multisensory technologies.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

GR conceived and developed the initial draft. FP revised the initial draft. SS, DD, and FP worked with GR to enhance the revised draft and develop it into the final draft. All authors have reviewed and approved the final manuscript as submitted.

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Development of Abstract Word Knowledge

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The development of children's word knowledge is an important testing ground for the embodied account of word meaning, which proposes that word meanings are grounded in sensorimotor systems. Acquisition of abstract words, in particular, is a noted challenge for strong accounts of embodiment. We examined acquisition of abstract word meanings, using data on development of vocabulary knowledge from early school to University ages. We tested two specific proposals for how abstract words are learned: the affective embodiment account, that emotional experience is key to learning abstract word meanings, and the learning through language proposal, that abstract words are acquired through language experience. We found support for the affective embodiment account: word valence, interoception, and mouth action all facilitated abstract word acquisition more than concrete word acquisition. We tested the learning through language proposal by investigating whether words that appear in more diverse linguistic contexts are earlier acquired. Results showed that contextual diversity facilitated vocabulary acquisition, but did so for both abstract and concrete words. Our results provide evidence that emotion and sensorimotor systems are important to children's acquisition of abstract words, but there is still considerable variance to be accounted for by other factors. We offer suggestions for future research to examine the acquisition of abstract vocabulary.

Keywords: age-of-acquisition, concreteness, valence, interoception, abstract vocabulary, mouth action, affective embodiment, contextual diversity

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INTRODUCTION

The embodied account of word meaning proposes that children's concepts emerge out of sensorimotor interactions (Glenberg and Gallese, 2012; Glenberg, 2015) and there is considerable evidence, particularly for concrete concepts, that this is the case (Smith et al., 2007). However, a challenge for the embodied account of word meaning, and particularly for strong accounts of embodiment, is to explain the acquisition of words that refer to abstract concepts (Borghi et al., 2017; Pexman, 2017). Specifically, if abstract word meanings are not experienced through the senses, how can children acquire them? In spite of the absence of a physical referent, children do learn the meanings of abstract words like *love* and *help*. According to a multimodal approach to word meaning, words can be learned in multiple ways, including sensory, motor, emotion, social, and linguistic information associated with the referent (Kousta et al., 2011; Borghi et al., 2019); thus providing several mechanisms by which abstract words might be acquired. The purpose of the present paper was to test these theoretical claims with a developmental approach, by examining the influence of different types of information on acquisition of abstract and concrete word meanings across childhood and into young adulthood.

Abstract words do not tend to have a clear, perceptible referent (Borghi et al., 2017; Ponari et al., 2020). They are more detached from sensorimotor experience. In addition, their meanings are less stable over time and are more influenced by life experience and situations (Barsalou et al., 2018). Brysbaert et al. (2014) described concrete words as those that can be experienced through one of the five senses (e.g., *sweet*, *jump*, *couch*) and abstract words as those for which the meaning depends on language as they cannot be experienced through the senses (e.g., *justice, dare*). Brysbaert and colleagues collected concreteness ratings for over 40,000 words, on a rating continuum ranging from very abstract (1) to very concrete (5). Many studies have used these ratings to categorize abstract words as those with concreteness ratings < 3 and concrete words as those with concreteness ratings ≥ 3 (Ponari et al., 2016, 2020; Lund et al., 2019).

Development of Abstract Language

Ponari et al. (2016) reviewed the very limited extant research on abstract vocabulary acquisition and observed that for children between the ages of 7–8 and 9–10 years there was a surge in the quantity of abstract word meanings they understood. Ponari et al. (2016) made these observations based on subjective ratings of age-of-acquisition (age when given words are learned; AoA; Kuperman et al., 2012) and concreteness (Brysbaert et al., 2014), which were available for a set of 13,226 words. They confirmed that abstract words are, on average, rated as being acquired later than concrete words, with only 10% of a 4-year-old's estimated vocabulary consisting of words referring to abstract concepts. They further reported that the proportion of abstract words acquired expands rapidly across middle childhood, to an estimated 40% of total vocabulary by age 12. The question of how children acquire these abstract word meanings is, as yet, unanswered, but there are two main proposals that have so far been tested in developmental studies. We review these next.

Acquisition of Abstract Vocabulary – Specific Theoretical Proposals

Affective Embodiment Account

The *affective embodiment account* (Kousta et al., 2011; Borghi et al., 2017) provides a way in which the meanings of abstract words could be grounded in bodily experience and thus is consistent with the broad notion of embodiment. The proposal is that emotional experience is key to the grounding of the representation of abstract concepts (Kousta et al., 2011). By the affective embodiment account, the emotion aspects of word meanings provide a way for children to begin to build representations of abstract concepts. The meanings of children's first abstract words may be grounded in felt experience, such as associating *love* with a feeling of being cuddled. Emotion words can provide children with "essence placeholders" (Shablack et al., 2020, p. 1538) that categorize their bodily experiences.

There is evidence to support the claim that abstract words are grounded in emotional experience. Altarriba et al. (1999) noted that the valence of words (positive, neutral, negative) interacted with concreteness and found that although valenced words were rated low on concreteness (like other abstract words), they were rated high on imageability and context availability. Relatedly, the results of a semantic categorization study with adults demonstrated that emotion information facilitated processing of abstract words, whereas sensorimotor information facilitated processing of concrete words (Newcombe et al., 2012). Similarly, Pexman and Yap (2018) found that valence information (positive or negative) facilitated adults' semantic decisions to abstract words, but not to concrete words.

Valence

There are many aspects to emotional experience, but the developmental research has thus far tended to focus on valence information. Evidence that valence may be related to vocabulary acquisition, and may be particularly important for abstract vocabulary acquisition, was reported in previous studies that have analyzed AoA norms (Kousta et al., 2011; Ponari et al., 2016). Kousta et al. (2011) reported that abstract valenced words (regardless of polarity) were rated as being acquired earlier than abstract words that were not valenced (neutral words). Using different AoA norms, Ponari et al. (2016) confirmed the relationship between concreteness (Brysbaert et al., 2014) and AoA (Kuperman et al., 2012) across more than 13,000 words. That is, Ponari et al. (2016) confirmed that abstract words are rated to be acquired later than concrete words. Importantly, they also found an interaction between valence (Warriner et al., 2013) and concreteness for AoA ratings. They found that for abstract words in particular, those that are valenced (both positive and negative) were rated as being acquired earlier than those that are neutral.

Ponari et al. (2016) also examined the processing of abstract and concrete words in an auditory lexical decision task with children aged 6 to 12 years. They found that valence affected response accuracy specifically for abstract words, and only in children aged 8–9 years. They did not find valence effects in the younger children (6–7 years) and noted that response accuracy for the younger children was very low, suggesting the children did not know many of the words. Further, valence effects were not found in the responses of the older children (10–11 years); this was attributed to increased knowledge of neutral abstract word meanings in this older group. The authors concluded that their results were consistent with the proposal that emotion (as captured by the valence dimension) provides a bootstrapping mechanism for learning the meanings of abstract words. Similarly, in a recent vocabulary learning experiment, Ponari et al. (2020) found that 7–9 year old children were able to provide more accurate definitions for valenced words than neutral words.

In a closely related study, Lund et al. (2019) further tested the predictions of the affective embodiment account by investigating valence and concreteness effects in children's reaction times on an auditory lexical decision task. Their participants were children aged 5-, 6- and 7-years. They found a facilitatory effect of valence in the responses of both 6- and 7-year-olds. This sensitivity to emotional information was not present in the 5-year-olds. There was also an interaction of valence and concreteness in the responses of the 6-year-olds, which involved a processing advantage for positive abstract words compared to neutral abstract words, providing some limited support for the affective embodiment prediction that emotion information plays a stronger role in the processing of abstract words than concrete words. Lund et al. (2019) found effects of valence at an earlier age than in the study by Ponari et al. (2016), suggesting that valence information might support children's early acquisition of abstract vocabulary.

Finally, Kim et al. (2020) tested a different cognitive process, children's recognition memory, for the interaction of valence and concreteness. They presented 7- to 8-year-old children with spoken word stimuli that varied on both valence and concreteness. In a recognition memory test the same day, they assessed children's accuracy in identifying the words they had heard earlier. They found the predicted interaction of valence and concreteness in children's recognition memory accuracy: children were more accurate in their memory for negative words than for neutral words, but only for abstract meanings; valence had no effect on memory for concrete meanings. Thus, the Kim et al. findings were consistent with those described above; all of these findings have been taken as support for the predictions of affective embodiment, wherein children are proposed to ground abstract word meanings in emotional systems.

The findings from the behavioral studies reviewed above do provide some support for the affective embodiment account, but there are certainly limitations to this work, and other aspects of the findings suggest that the picture may be more complex. First, in order for Lund et al. (2019) to provide words that were known to young children, the 'abstract' words selected for the study were relatively less abstract than those presented in other studies (e.g., Ponari et al., 2016). Secondly, although Ponari et al. (2020) found evidence of valence in the definition task they used with 7–9 year old children, they also found no differences in accuracy for valenced versus neutral words on an auditory lexical decision task, and there was no impact of valence in the definitions provided by the 9–10 year-old children. Vigliocco et al. (2018) noted that valence information does not appear to support abstract vocabulary acquisition beyond the age of 9. The authors concluded that this is evidence of a hybrid or multimodal view of semantic representation, with both embodied and linguistic features. Third, the developmental studies conducted so far have examined the construct of emotion only in terms of valence information. Yet there is much more to emotional experience than the evaluative aspect captured by valence. In the present study, we investigated the roles of several other aspects of emotional experience in development of abstract word knowledge.

Arousal

Arousal is proposed to be a dimension of emotional experience, involving the degree of excitement or intensity associated with word meaning (Russell, 1980). The effects of arousal on children's abstract vocabulary acquisition have not yet been examined. but the dimension might capture some of the more visceral aspects of emotional experience than those associated with valence.

Interoception

Similarly, interoception captures the various sensations *inside* the body (Barsalou, 1999; Barsalou and Wiemer-Hastings, 2005; Borghi et al., 2017; Connell et al., 2018; Harpaintner et al., 2018). To test the proposal that abstract concepts are grounded through interoception, Connell et al. (2018) examined a large set of modality-specific sensorimotor experience ratings (an early iteration of the Lancaster Sensorimotor Norms, Lynott et al., 2020) and compared strength of modality-specific experience for abstract and concrete words. They found that interoceptive strength ratings were higher for abstract than concrete word meanings and concluded that interoception is more important to the representations of abstract concepts than concrete concepts. Some, but not all, of this difference in interoceptive strength between abstract and concrete words could be attributed to the fact that emotions, which tend to be abstract, have higher interoception ratings. Similarly, Zdrazilova et al. (2018) used a face-to-face task to explore the words and gestures that people used to communicate abstract and concrete word meanings. They found that interoceptive states were frequently referenced as participants described abstract (but not concrete) meanings.

Mouth Action

In addition, Anna Borghi and colleagues have proposed that the mouth motor system, by virtue of its fundamental role in both overt and covert language production, is important to abstract meanings (e.g., Granito et al., 2015; Barca et al., 2017; Borghi, 2020). For instance, Barca et al. (2020) conducted a semantic categorization task with children in grade 3 (approximately 8–9 years of age) with concrete, abstract, and emotion word stimuli. The results showed that children who had used a pacifier extensively in early childhood were particularly slow to respond to abstract words. The inference was that extensive pacifier use disrupts mouth-associated social and linguistic experiences, and that these are important to abstract vocabulary acquisition. Thus, Barca et al. concluded that mouth effectors are important for abstract vocabulary acquisition (see also Barca et al., 2017).

Head Action

It is also possible that head actions (distinct from actions of the mouth/throat) tend to be engaged in emotions and when experiencing the meanings of abstract words, because many abstract meanings involve social, cognitive, and internal states and relations that are likely to be affected through movements of the head and eyes. Indeed, Connell (2021; see also Banks and Connell, 2021); reported that head (non-mouth) action strength was important to the representations derived for many abstract concepts from the Lancaster Sensorimotor Norms. There is also some neuroimaging evidence to suggest that abstract word meaning may be grounded to some extent in head-related sensorimotor experience. Dreyer and Pulvermüller (2018) identified stronger activation in motor regions associated with the face during passive reading of abstract mental words (e.g., *logic*) relative to activation in motor regions associated with hand actions. As such, head action strength might also be important for abstract vocabulary acquisition; however, the association between head action and abstract word representation has yet to be tested developmentally.

Thus, there are several ways in which emotional experience could be measured, beyond valence, and by which the affective embodiment account could be tested more fully. In addition, Borghi et al. (2017) noted that affective embodiment accounts for the grounding of valenced abstract concepts but does not provide a clear explanation for representation of abstract concepts that do not have emotional connotations. Therefore, there is a need for research that considers other mechanisms, beyond emotion, that might support word learning into adolescence and adulthood. One other mechanism that has been proposed to support abstract vocabulary acquisition is language experience.

Learning Through Language Proposal

There are numerous proposals that language is particularly important to the meanings of abstract concepts (e.g., Paivio, 1991; Borghi et al., 2019; Borghi, 2020; Dove et al., 2020). In the developmental context, it has been proposed that abstract words are learned through linguistic cues. For instance, Gleitman and colleagues (Gleitman, 1990; Gleitman et al., 2005; Papafragou et al., 2007) proposed the *syntactic bootstrapping hypothesis*, by which syntactic information is used to support word learning. Gleitman (1990) proposed that children initially learn words through a word-to-world mapping, pairing a word with a referent in the environment. Once children have acquired knowledge about regularities in language they begin to infer word meanings from linguistic context, a ‘structure-to-world’ pairing which is particularly helpful for learning abstract words, since these tend not to have observable referents. The proposal of the syntactic bootstrapping hypothesis is that children can only learn abstract words after they have enough sophisticated language knowledge to match an event with the appropriate syntactic structure.

In addition to syntactic cues, children may also learn word meanings from situational context (Shablack et al., 2020) and from regularities in the ways words are used and co-occur in language (Andrews et al., 2009; Hills et al., 2010). The proposal that abstract words are learned through language requires that children must have first learned at least some concrete concepts with which to ground the meaning of new abstract words that do not have a sensorimotor component. This co-occurrence or distributional approach does not emphasize the need to develop specific syntactic structures with which to scaffold later learning, but rather proposes that linguistic knowledge can provide an additional grounding for word meaning in the absence of experiential sensory, motor, or emotion information.

Lund et al. (2019) provided some evidence for the role of language in abstract vocabulary acquisition. They found that in an auditory lexical decision task, children’s response times to neutral (non-valenced) abstract words were related to the children’s language skills, such that children with more advanced language skills responded more quickly to neutral abstract words than did children with weaker language skills. They took this as evidence for what they termed the *language competence hypothesis*: the proposal that when words do not have the benefit of additional information from sensory, motor, or emotion attributes children draw upon language experience to learn those word meanings. Vigliocco et al. (2009) also predicted that language experience, and in particular distributional information, may be more important for abstract words than for concrete words, since abstract meanings lack sensory and motor contingencies. Similarly, Ponari et al. (2020) suggested that the results of their word learning experiment provided evidence of learning through language. They found that while 9- to 10-year-old children learned the meanings of new abstract words they did not show evidence of experiential benefit (i.e., through emotion) in their meaning definitions. In contrast, valence played a role in the definitions provided by younger children (aged 7- to 9 years), who could define valenced abstract words more accurately than neutral abstract words.

Another aspect of language experience that may be important to children’s abstract vocabulary acquisition is the diversity of contexts in which words are experienced. Hills et al. (2010) investigated why children learn some words earlier than others. They examined the diversity of contexts in the learning environment and found that a word’s contextual diversity – the number of unique word types with which a word co-occurs in the child’s language environment – predicted the order of acquisition. They found that early word acquisition was influenced by *preferential acquisition*, in which a word is more likely to be learned if it is in close proximity to many other words in the learning environment. Secondly, they found that word learning was influenced by the *lure of associates*: a word was more likely to be learned if it is related to other words the child already knows. The lure of associates principle is consistent with the proposal that abstract words are acquired through language. If first (concrete) words are learned through observation and grounded through links to sensory, motor, and emotion experiences, later words can then be grounded through language, via the lure of associates. Hills et al. did not examine the effects of contextual diversity for acquisition of abstract words specifically, but we did so in the present study.

This Paper

The purpose of the present paper was to test these various proposals about factors that are important to children’s abstract vocabulary acquisition, using a large-scale vocabulary acquisition dataset that spans early school to University ages (Dale and O’Rourke, 1981; as updated in Brysbaert and Biemiller, 2017). We tested whether each of the following factors predict vocabulary acquisition: valence, arousal, interoceptive strength, mouth action strength, head action strength, and diversity of language context. We also tested whether each of these factors interacts with concreteness, since each proposal holds that the factor should have stronger effects for abstract than concrete word acquisition.

MATERIALS AND METHODS

The methodology of the present study involved analyses using five existing datasets. The dependent measure in our analyses was the test-based age of acquisition (AoA) data that were originally reported by Dale and O'Rourke (1981). The Dale and O'Rourke (1981) data estimated AoA by objective means, testing children's vocabulary knowledge across school grades and including over 31,000 unique words. Each word's AoA in those data is equal to the lowest grade in which it is known to an estimated 50–70% of students, based on children's responses to three-alternative multiple-choice tests and corrected for guessing. Brysbaert and Biemiller (2017) updated and expanded the Dale and O'Rourke (1981) data so that they offered vocabulary estimates for grades 2, 4, 6, 8, 10, 12, 13, and 16 (the latter two are university levels). Items in the Brysbaert and Biemiller (2017) dataset may occur more than once with different ages, reflecting when different meanings of a word were acquired. In these cases, we used the AoA of the earliest acquired meaning in our analysis.

Our predictor variables included two control variables, word frequency, which was included in analyses to control for the known relationship between frequency and AoA (log subtitle frequency; Brysbaert and New, 2009) and word length. In addition, we had seven key semantic predictors: ratings of concreteness (the degree to which a word refers to something that can be experienced through one of the five senses; Brysbaert et al., 2014), ratings of word valence (the degree to which reading a word makes you feel unhappy or happy) and arousal (the degree to which reading a word makes you feel calm or excited; Warriner et al., 2013), three measures from the Lancaster Sensorimotor Norms: ratings of interoceptive strength (the degree to which a concept is experienced by internal sensations of the body), mouth action strength (the degree to which a concept is experienced by mouth/throat actions) and head action strength (the degree to which a concept is experienced by head actions excluding the mouth; Lynott et al., 2020), and semantic diversity (the extent to which a word appears in diverse contexts; Hoffman et al., 2013).

RESULTS

We extracted test-based age of acquisition norms from Brysbaert and Biemiller (2017), which were derived from the data in Dale and O'Rourke (1981) Living Word Vocabulary, concreteness ratings (Brysbaert et al., 2014), valence and arousal ratings (Warriner et al., 2013), semantic diversity ratings (Hoffman et al., 2013), interoceptive, head, and mouth strength ratings (Lynott et al., 2020), log subtitle frequency (Brysbaert and New, 2009) and length. In total there were 9,916 items for which we had values for all variables of interest. We calculated correlations between all variables of interest, as well as the variables of positive valence (i.e., all variables with valence greater than or equal to 5), negative valence (i.e., all variables with valence less than or equal to 5) and valence extremity (i.e., the absolute value of the valence rating from 5, the neutral point on the scale). All variables were significantly correlated ($p < 0.01$) with the exception of head and mouth perceptual strength, which were not correlated with test-based AoA, nor was mouth action strength correlated with valence (**Table 1**).

We tested theories of abstract word acquisition with a hierarchical regression model. In the first stage we entered all predictors of test-based AoA. Predictors in the first stage accounted for 42.63% of variance in test-based AoA. We observed significant effects for all predictors with the exception of length and head and mouth action strength (**Table 2**). We then added interactions between concreteness and each semantic predictor variable to assess the affective embodiment account and learning through language theories of abstract word acquisition. There was a significant improvement in model fit with the addition of the interactions (**Table 2**), with the interactions accounting for an additional 0.75% of variance in test-based AoA.

First, the affective embodiment account was tested via an interaction between concreteness and valence in predicting test-based AoA. Valence was entered as a linear and a quadratic term due to the bipolar nature of the scale (e.g., 1 = negative, 9 = positive, 5 = neutral). We observed a significant interaction between concreteness and the quadratic term of valence on test-based AoA while holding all other parameters constant, $b = 1.48$, $t(9898) = 7.54$, $p < 0.001$, such that neutral abstract words were learned significantly later than neutral concrete words. The interaction between concreteness and valence on test-based AoA is depicted in **Figure 1A**.

To further test aspects of emotional experience that could be related to abstract word acquisition, we examined interactions between concreteness and arousal, interoceptive strength, head action strength, and mouth action strength. We observed a significant interaction between concreteness and interoceptive strength on test-based AoA while holding all other parameters constant, $b = 0.13$, $t(9898) = 3.46$, $p = 0.001$, such that abstract words with low interoceptive strength were learned later than concrete words with low interoceptive strength; abstract words with high interoceptive strength were not acquired significantly later than concrete words with high interoceptive strength. The interaction between concreteness and interoceptive strength on test-based AoA is depicted in **Figure 1B**.

There was also a significant interaction between concreteness and mouth action strength on test-based AoA while holding all other parameters constant, $b = 0.06$, $t(9898) = 2.15$, $p = 0.031$, such that abstract words with lower mouth action strength were learned later than concrete words with lower mouth action strength; abstract words with higher mouth action strength were not acquired significantly later than concrete words with higher mouth action strength. The interaction between concreteness and mouth action strength on test-based AoA is depicted in **Figure 1C**.

We observed no significant interaction between concreteness and arousal on test-based AoA while holding all other parameters constant, $b = -0.00$, $t(9898) = -0.05$, $p = 0.959$ (see **Figure 1D**). Nor was there a significant interaction between concreteness and head action strength, $b = 0.01$, $t(9898) = 0.32$, $p = 0.746$ (see **Figure 1E**).

Finally, we tested the learning through language proposal via an interaction between concreteness and semantic diversity in predicting test-based AoA. We observed no significant interaction between concreteness and semantic diversity, $b = 0.00$, $t(9898) = 0.08$, $p = 0.936$ (see **Figure 1F**).

TABLE 1 | Means, standard deviations, and correlations of all variables of interest.

Variable	*M*	*SD*	1	2	3	4	5	6	7	8	9	10	11	12
(1) Test-based AoA	8.63	4.04												
(2) Length	7.48	2.35	0.23**											
(3) Frequency	1.73	0.92	−0.60**	−0.36**										
(4) Concreteness	3.21	1.05	−0.32**	−0.29**	0.10**									
(5) Valence	5.09	1.27	−0.18**	−0.02	0.20**	0.09**								
(6) Positive Valence	5.96	0.70	−0.19**	0.04**	0.23**	−0.13**	1.00**							
(7) Negative Valence	3.92	0.83	0.03*	−0.08**	−0.10**	0.18**	1.00**	NA						
(8) Valence Extremity	1.03	0.75	−0.10**	0.06**	0.15**	−0.16**	−0.08**	1.00**	1.00**					
(9) Arousal	4.19	0.89	0.03**	0.10**	0.04**	−0.17**	−0.17**	0.28**	−0.42**	0.35**				
(10) Interoceptive Strength	1.03	0.90	0.03**	0.07**	0.10**	−0.41**	−0.11**	0.36**	−0.40**	0.38**	0.31**			
(11) Mouth Action Strength	1.29	0.94	−0.01	0.03**	0.10**	−0.18**	0.03**	0.22**	−0.20**	0.21**	0.14**	0.28**		
(12) Head Action Strength	2.29	0.73	−0.06**	0.11**	0.14**	−0.19**	0.09**	0.26**	−0.21**	0.22**	0.15**	0.25**	0.25**	
(13) Semantic Diversity	1.56	0.35	−0.21**	−0.04**	0.39**	−0.38**	0.04**	0.07**	−0.02	0.05**	0.02	0.19**	0.07**	0.09**

*M and SD are used to represent mean and standard deviation, respectively. AoA, Age of Acquisition. *Indicates $p < 0.05$. **Indicates $p < 0.01$.*

TABLE 2 | Hierarchical regression predicting test-based AoA using all variables of interest ($N = 9{,}916$).

Variables	*b*	*b* 95% CI [LL, UL]	sr^2	Fit	Difference
Intercept	6.24**	[6.19, 6.29]			
Length	0.02	[−0.04, 0.08]	0.000		
Frequency	−1.47**	[−1.54, −1.40]	0.109		
Concreteness	−1.45**	[−1.52, −1.38]	0.090		
Valence - Linear	1.79**	[1.42, 2.17]	0.005		
Valence - Quadratic	−2.01**	[−2.39, −1.63]	0.006		
Arousal	0.11**	[0.06, 0.17]	0.001		
Interoceptive Strength	−0.13**	[−0.19, −0.06]	0.001		
Mouth Action Strength	−0.05	[−0.10, 0.01]	0.000		
Head Action Strength	−0.01	[−0.07, 0.05]	0.000		
Semantic Diversity	−0.48**	[−0.54, −0.41]	0.012		
				R^2 = 0.426**	
Intercept	6.36**	[6.29, 6.42]			
Length	0.02	[−0.04, 0.08]	0.000		
Frequency	−1.47**	[−1.54, −1.41]	0.109		
Concreteness	−1.42**	[−1.49, −1.35]	0.085		
Valence - Linear	1.48**	[1.10, 1.86]	0.003		
Valence - Quadratic	−1.71**	[−2.09, −1.33]	0.004		
Arousal	0.09**	[0.03, 0.15]	0.001		
Interoceptive Strength	−0.07*	[−0.14, −0.00]	0.000		
Mouth Action Strength	−0.10**	[−0.16, −0.04]	0.001		
Head Action Strength	0.02	[−0.05, 0.08]	0.000		
Semantic Diversity	−0.48**	[−0.55, −0.42]	0.012		
Concreteness by Valence - Linear	−1.56**	[−1.95, −1.16]	0.003		
Concreteness by Valence - Quadratic	1.48**	[1.10, 1.87]	0.003		
Concreteness by Arousal	−0.00	[−0.06, 0.06]	0.000		
Concreteness by Interoceptive Strength	0.13**	[0.05, 0.20]	0.001		
Concreteness by Mouth Action Strength	0.06*	[0.01, 0.12]	0.000		
Concreteness by Head Action Strength	0.01	[−0.05, 0.07]	0.000		
Concreteness by Semantic Diversity	0.00	[−0.06, 0.06]	0.000		
				R^2 = 0.434**	ΔR^2 = 0.007**

*A significant b-weight indicates the semi-partial correlation is also significant. b represents unstandardized regression weights. sr^2 represents the semi-partial correlation squared. LL and UL indicate the lower and upper limits of a confidence interval, respectively. *Indicates $p < 0.05$. **Indicates $p < 0.01$.*

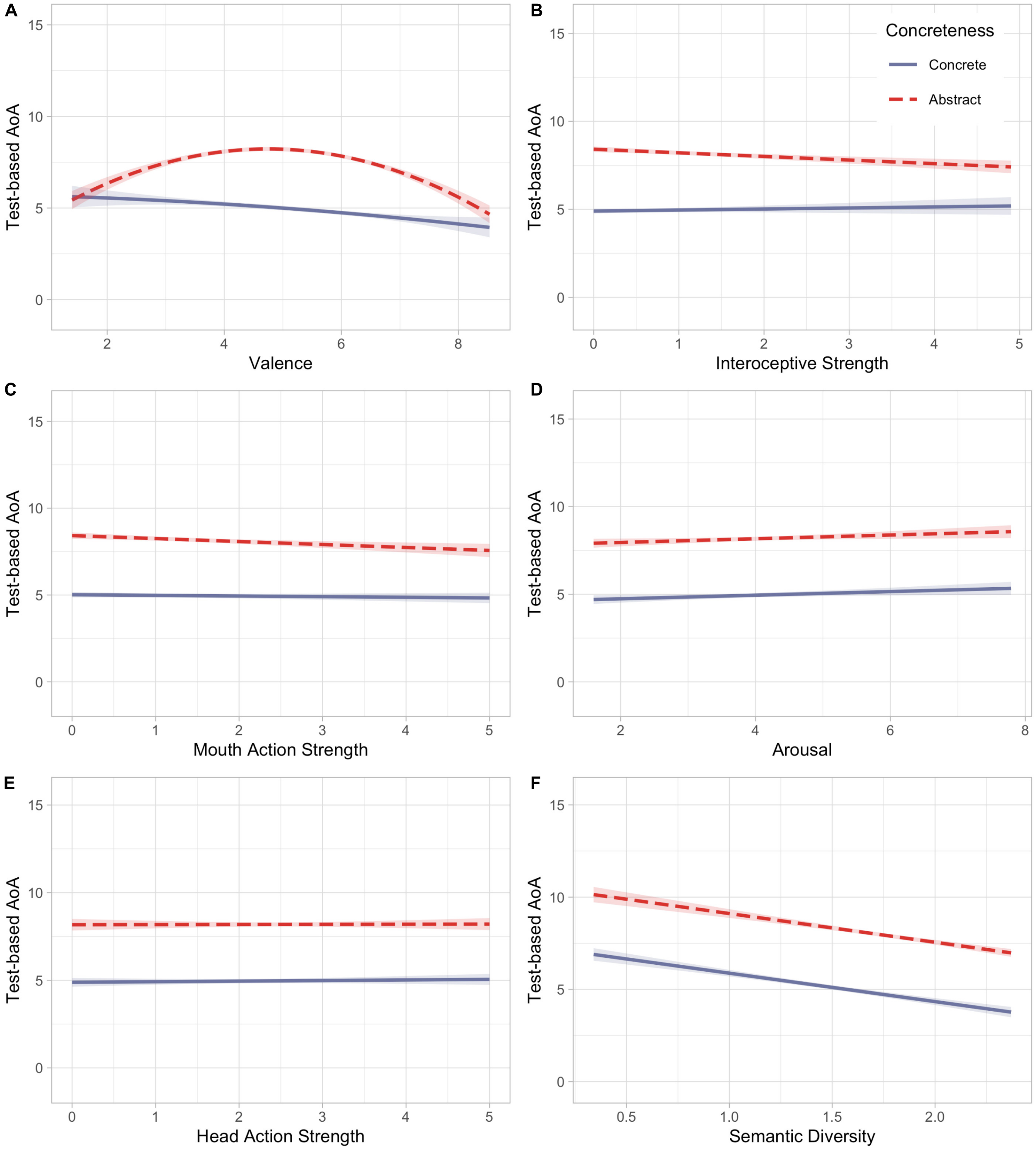

FIGURE 1 | AoA, Age of Acquisition. Plots depict partial residuals of the interaction between concreteness and **(A)** Valence, **(B)** Interoceptive Strength, **(C)** Mouth Action Strength, **(D)** Arousal, **(E)** Head Action Strength and **(F)** Semantic Diversity in predicting AoA. All plots represent the interaction relationship when other variables in the model are held constant.

DISCUSSION

The purpose of the present study was to investigate the degree to which acquisition of abstract word knowledge across childhood and into young adulthood is related to the emotional, sensorimotor, and linguistic information associated with a word's referent. We tested specific proposals for how abstract words are acquired. According to the affective embodiment hypothesis, emotional experience is key to learning the meanings of abstract words (Kousta et al., 2011) because many abstract words refer to internal states that can create an emotional experience (Ponari et al., 2016). According to the learning through language proposal, abstract word meanings are acquired through experience with language.

In the present study we examined several aspects of emotional experience that could be relevant to the acquisition of abstract words. Kousta et al. (2011) found that valence alone does not capture completely the meaning of abstract words. Therefore, in addition to valence, we expanded the emotional properties to include measures of word arousal and interoceptive strength. To examine associated sensorimotor experiences we examined mouth and head action strength. Therefore, the affective embodiment account was tested by examining the relationship between word valence and word arousal with test-based AoA, and also by testing whether these relationships varied for abstract and concrete words. We observed a significant quadratic relationship between valence and test-based AoA for abstract words, suggesting that emotional information (both positive and negative) is more important for abstract word acquisition than for concrete word acquisition. Furthermore, we observed a significant interaction between interoception strength and concreteness on test-based AoA, such that abstract words associated with less interoceptive experience are acquired later than concrete words with less interoceptive experience, whereas there is less difference in the acquisition of abstract and concrete words associated with more interoceptive experience. Additionally, we observed a significant interaction between mouth action strength and concreteness on test-based AoA, with abstract words that had lower mouth action strength ratings being acquired later than concrete words with lower mouth action strength ratings, and less difference in the acquisition of abstract and concrete words with more mouth action strength. This would suggest that mouth effectors are more important for abstract word acquisition than for concrete word acquisition, consistent with arguments made by Borghi and colleagues (Barca et al., 2017, 2020; Borghi et al., 2019) about the role of mouth experience in grounding abstract word meanings. Thus, valence, interoceptive strength, and mouth action strength facilitate acquisition of abstract words, and are less important for acquisition of concrete words, consistent with the predictions of the embodiment account. These results provide further evidence to support the claim that abstract words are grounded in emotional and associated sensorimotor experiences.

Borghi et al. (2017) argued that one limitation of the affective embodiment account is that the proposed role of valence does not account for all the mechanisms underlying the acquisition of abstract concepts. The current analysis shows that additional conceptualizations of emotional experience, namely interoceptive and mouth action strength, can further explain the development of abstract word meanings as grounded in a more broadly defined operationalization of emotion. In addition, as proposed in Borghi and Binkofski (2014) *words as social tools* (WAT) view, we found that abstract concept acquisition is associated with mouth action strength. Borghi et al. (2017) proposed that the mechanism of subvocalization is more important for abstract than concrete words, as evidenced in the current analysis by increased mouth action strength for abstract words.

The learning through language proposal would suggest that the meanings of abstract words and concepts can be acquired through language experience. This proposal is consistent with both the distributional theory of semantics (Andrews et al., 2009) and the syntactic bootstrapping hypothesis (Gleitman et al., 2005). It was predicted that linguistic distribution information may be more important for abstract words than for concrete words, since abstract meanings lack sensory and motor contingencies (Vigliocco et al., 2009). We tested the specific notion that contextual diversity (operationalized here as the semantic diversity variable computed by Hoffman et al., 2013) would facilitate abstract vocabulary acquisition more than concrete vocabulary acquisition. We observed a significant relationship between semantic diversity and AoA, but this relationship did not vary for abstract and concrete words. Therefore, consistent with the findings from Hills et al. (2010), early word acquisition was influenced by preferential acquisition, in that words, both concrete and abstract, are learned earlier when they are present in more diverse contexts in the learning environment. This suggests that exposure to word meanings in diverse linguistic contexts is important to both abstract and concrete word acquisition. As contextual diversity did not disproportionately affect the acquisition of abstract words, the current findings did not provide evidence for the view that abstract word learning was influenced by lure of associates, or that abstract words are more likely to be learned if they are related to other words the child already knows. Rather, the current findings suggest that all words, both concrete and abstract, are learned earlier when they have been experienced in diverse contexts, presumably because their meanings have greater opportunities to be linked to already known words.

In the *language and situated simulation* (LASS; Barsalou et al., 2008) multiple representations view, both simulated modal (sensory, motor, and emotion) and linguistic systems can support learning. The current findings are consistent with this view, in that emotion systems are important to the learning of abstract words, and linguistic systems support both concrete and abstract word learning. Notably, we did not test whether other aspects of language use, or acquisition of specific language structures (e.g., relational terms) might be particularly important to abstract vocabulary acquisition. This will be an important issue for future research. We turn to other such topics next.

Limitations and Future Directions

One limitation of our study is that we examined AoA starting at grade 2. Therefore, there is data missing from our analysis concerning the very early stages of language development. There is evidence that most children have acquired at least some emotion words by age 2 (Wellman et al., 1995) and theories of acquisition will need to account for this early acquisition. To address this limitation, we examined the characteristics of children's earliest abstract words, based on information extracted from the Wordbank database[1]. Wordbank provides

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[1] http://wordbank.stanford.edu

information about vocabulary acquisition for children under age 3 (Frank et al., 2017). The database provides vocabulary norms and aggregate data on the proportion of children at a particular age who know a specific word, based on over 42,000 administrations of the MacArthur-Bates Communicative Development Inventories (CDIs). The CDIs are widely used parent-report instruments to gather data about early language acquisition. Of the nearly 600 words in this database, 96 had concreteness ratings < 3, based on the Brysbaert et al. (2014) concreteness norms. Thus, these are children's earliest abstract words. Interestingly, none of these 96 words were nouns. Instead, children's early-acquired abstract words were closed-class words including determiners (e.g., *the, all*), conjunctions (e.g., *and, or*), prepositions (e.g., *for, to, by, with*), exclamations (e.g., *yes, no, hi, bye*), and pronouns (e.g., *this, that, they, it*); as well as open-class words including adverbs (e.g., *there, away, how, now, why, better*), adjectives (e.g., *yucky, careful, pretty*), and verbs (e.g., *be, like, think*). We used ratings from Warriner et al. (2013) to examine the valence of these early abstract words. Valence ratings were available for 42 of these words, including seven words with negative valence ratings, 18 words with neutral valence ratings, and 17 words with positive valence ratings. In sum, children do present with knowledge of a variety of abstract words before age 3, including several that do not have associated emotion information, suggesting that acquisition of these earliest words is not entirely explained by affective embodiment. Those early abstract words that are associated with emotion information tend not to be negatively valenced. Indeed, there is evidence that children tend to hear more positive than negative words in child-directed speech which may reflect a tendency of parents and caregivers to avoid negative language with children, especially in the early years (Ponari et al., 2016).

As described in the Results section above, the omnibus model accounted for 43.4% of variance in test-based AoA, implying that while we have identified some of the variables that predict vocabulary acquisition, there is still considerable variance to be accounted for by other factors. One possible explanation concerns the heterogeneity of both abstract and concrete concepts; for instance, abstract words refer to a wide variety of concepts, including words that refer to emotions, mental states, interospections, social concepts, etc. (Kiefer and Harpaintner, 2020; Muraki et al., 2020b). Desai et al. (2018) proposed four categories of abstract words: numerical, emotional, morality, and theory of mind. Similarly, Borghi et al. (2019) also provided evidence for four types of abstract words: philosophical/spiritual, physical/spatial/quantitative, self-sociality, and emotive/inner states. In two recent studies, Muraki and colleagues found that different types of abstract verbs can be distinguished in terms of associated behavioral and neural responses (Muraki et al., 2020a,b). The inference is that different types of abstract words are associated with different combinations of linguistic, sensory, emotion, and other information. We did not attempt to capture this variability in the present analyses, but it is an important topic for future research.

While the abstract/concrete distinction has historically been conceptualized as a dichotomy, there is considerable evidence that it is more accurately characterized as a continuum. By the affective embodiment account, emotion concepts are assumed to contain both abstract and concrete elements and indeed ratings of emotion concepts suggest that they tend to fall more toward the middle of the abstract-concrete continuum (Altarriba and Bauer, 2004; Winkielman et al., 2018). Barsalou et al. (2018) proposed to move beyond the concrete/abstract distinction altogether and to view all concepts within a *situated conceptualization framework,* where representations are multimodal and different kinds of concepts draw on different situations and contexts.

Barsalou et al. (2018) argued that abstract concepts are not well served if we define them based on what they are *not* (i.e., not attached to a physical entity that is perceptible in the real world). According to Barsalou et al.'s (2008) LASS view, multiple systems underlie our knowledge of concepts. LASS focuses on the linguistic and the simulation systems, which interact continuously. In this view, all concepts involve an interaction between the linguistic and perceptual systems (sensory, motor, and emotive). Barsalou et al. argued that words serve as "pointers" to the object, entity, or situation to which they refer. In this way, many of the traditional lexical measures – naming, lexical decision, semantic decision tasks – may not be the best measures of word meaning retrieval, since they involve simple responses to words presented without context and thus may not tap the rich meanings to which those words point. This may be particularly true for abstract concepts which can involve a simulation of an entire situation. A relatively "abstract" concept such as *justice,* when simulated, could parse into a rather concrete situation: a courtroom with a judge, an obvious criminal and victim. Contrarily, when considering the broader context, even an undeniably "concrete" concept such as *table* could evoke a complexity of abstractness when you consider a situation such as "all the stakeholders brought their issues to the *table*". In this situation there is no object present, but rather a simulation of an abstract situation.

There is evidence that our representations for concepts change with development and experience. A recent analysis showed that children's emotion concepts are initially quite concrete and then become more abstract across development (Nook et al., 2020). Nook et al. (2020) argued that since emotion concepts do not fit clearly into either abstract or concrete categories, they provide a unique testing ground for understanding development. Nook et al. found, for instance, that younger children tended to provide more situational examples for emotion concepts whereas older children provided increasingly complex definitions including synonyms. Nook et al. also found that acquisition of emotion words extends over a long developmental window: children's age of comprehension varied considerably across emotions (i.e., understanding at age 4 for *love* but not until age 10 for *calm*). When tapping characteristics beyond simple comprehension, such as definitions, synonyms, and situational examples, Nook et al. found that the variability was even greater, with successful comprehension at age 13 for concepts such as *hate*, *disappointed*, and *love*, but not until age 20 for *proud* and *annoyed*. They found that emotion comprehension plateaued earlier (around age 11) than did more complex emotion abstraction such as defining words and giving synonyms and situational examples, which did not plateau until around age 18.

We think that word association may be a useful next step to investigate children's vocabulary acquisition in a more contextual way. That is, human knowledge is highly associative, and by examining associations of different word meanings we might gain insight into the way that knowledge is represented. Based on an embodied theory of language development, word meanings are grounded and therefore learned through experience with the world. As such, this theory predicts that word associations would in general be related to the sensory, motor, or emotional experiences associated with the target word. Specifically, Kousta et al. (2011) proposed that emotion grounds the meaning of abstract words. Therefore, in a word association task, abstract words, particularly valenced abstract words, would be more likely to elicit valenced responses whereas concrete target words would likely elicit less valenced responses. This finding would support an embodied hypothesis, specifically that of grounding through emotion for abstract words. Contrarily, the proposal that abstract concepts are grounded in language would predict that the free associations to concrete and abstract cue words will not vary by valence. An examination of the associative structure of word meanings across development could help test these proposals.

CONCLUSION

The results of the present study show that even when frequency differences between concrete and abstract words are controlled, abstract words are later acquired. As Gleitman et al. (2005) noted, abstract words are "hard words". Our results show, however, that this challenge is eased when abstract words are associated with emotion, as measured by valence and interoceptive strength of the word's referent, or with mouth actions. We take this as evidence that even so-called 'abstract' word meanings can benefit from sensorimotor grounding. When that grounding is not present, other mechanisms are important. The task for future research is to further explicate those mechanisms, in order to develop robust theories of children's vocabulary acquisition, and of semantic representation more broadly.

DATA AVAILABILITY STATEMENT

Publicly available datasets were analyzed in this study. This data and the analysis scripts can be found here: https://osf.io/cywtv/. MacArthur-Bates Communicative Development Inventory data is available at: http://wordbank.stanford.edu/.

AUTHOR CONTRIBUTIONS

LR: conceptualization, writing – original draft preparation, and writing – review and editing. EM: analysis, writing – original draft preparation, and writing – review and editing. PP: conceptualization, and writing – review and editing. All authors contributed to the article and approved the submitted version.

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Six Weeks of Basketball Combined With Mathematics in Physical Education Classes Can Improve Children's Motivation for Mathematics

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This study investigated whether 6 weeks of basketball combined with mathematics once a week in physical education lessons could improve children's motivation for mathematics. Seven hundred fifty-seven children (mean age = 10.4 years, age range: 7–12 years) were randomly selected to have either basketball combined with mathematics once a week (BM) or to have basketball sessions without mathematics (CON). Children in BM and CON motivation for classroom-based mathematics were measured using the Academic Self-Regulation Questionnaire (SRQ-A) before (T0) and after the intervention (T1). Among the BM, levels of intrinsic motivation, feelings of competence, and autonomy were measured using the Post-Experimental Intrinsic Motivation Inventory (IMI) questionnaire acutely after a basketball session combined with mathematics and immediately after a session of classroom-based mathematics. BM had significantly higher acute levels of perceived autonomy (+14.24%, $p < 0.0001$), competencies (+6.33%, $p < 0.0001$), and intrinsic motivation (+16.09%, $p < 0.0001$) during basketball sessions combined with mathematics compared to when having classroom-based mathematics. A significant decrease in the mean for intrinsic motivation was observed from T0 to T1 for CON (−9.38%, $p < 0.001$), but not for BM (−0.39%, $p = 0.98$). BM had a more positive development in intrinsic motivation compared to CON from T0 to T1 ($p = 0.006$), meaning that BM had a positive influence on children's intrinsic motivation for classroom-based mathematics. This study indicates that basketball combined with mathematics is an intrinsically motivating way to practice mathematics, which also has a positive influence on children's general intrinsic motivation for mathematics in the classroom.

Keywords: motor-enriched learning, motivation, academic learning, children, intrinsic motivation, classroom-based mathematic, embodied cognition

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INTRODUCTION

Children's capacity to formulate, employ, and interpret mathematics, *mathematical literacy,* plays a central role in making well-founded judgments and decisions in life (Grinstein and Lipsey, 2001). Over the past decades, it has become more common to explore different learning approaches to stimulate children's mathematical learning to optimize the educational programs within mathematical subjects. Especially, intervention studies with focus on using physical activity to improve cognitive and academic performance have received a lot of attention (Sibley and Etnier, 2003; Best and Miller, 2010; Donnelly et al., 2016; Mavilidi et al., 2020).

Less focus has been aimed at the potentials of integrating physically active learning activities into the learning activities (Diamond, 2015; Pesce et al., 2016). The main purpose of the present study was to develop a model, which combines physical activity and mathematics in a play-based setting, and investigate how this play-based model affects children's motivation for mathematics.

An important contributor to academic achievement is motivation, which plays a central role in learning mathematics (Singh et al., 2002). Wienecke and Damsgaard (2020) describe how math combined with elements of basketball can be used as a practical model of play-based physical activity which can create a dynamic and enjoyable learning environment (Wienecke and Damsgaard, 2020). Valentini and Rudisill (2004) emphasize the possibilities of using basketball as an inclusive learning setting (Valentini and Rudisill, 2004). Mavilidi et al. (2018) used elements of basketball to support and reinforce the learning of English language concepts. The study indicates that children's joy and positive feelings rate high when having this learning setting (Mavilidi et al., 2018). Despite the promising data, no other previous study has focused on motivation and basketball combined with mathematics. Therefore, the present study aims to investigate how combining basketball with mathematics in a school setting affects children's motivation for mathematics.

Motivation that facilitates academic achievement can be facilitated by a positive learning environment and positive experiences with the academic task (Fortier et al., 1995; Singh et al., 2002). However, with age, students' reporting of enjoyable and stimulating school days decreases, especially between ages 11–15 (Gutman et al., 2010; Rasmussen et al., 2014).

According to the Self Determination Theory (SDT), there are different types of motivation with different levels of autonomy and different effects on academic achievement and development (Ryan and Deci, 2000). SDT distinguishes between four types of extrinsic motivation with various levels of external control and autonomy. These are: external regulation, where behavior is motivated by avoiding punishment; introjected regulation, where involvement is regulated by ego inflation through attaining success relative to others' expectations; identified regulation, where the individual recognizes and identifies with the value of the behavior; and integrated regulation, where the underlying value of an activity is not only recognized, but is also in coherence with other parts of the individual's deeper value system and identity (Deci and Ryan, 1985; Reis et al., 2000). Intrinsic motivation, on the other hand, is the behavior driven by reasons that are ingrained in the activity itself. Intrinsic motivation is the most autonomous type of motivation, and is a drive to do something because it is enjoyable and interesting more than doing something for extrinsic reasons and benefits. To experience competence, autonomy and relatedness are considered basic psychological needs, which must be fulfilled when doing an activity for sustaining the intrinsic motivation for that activity (Deci et al., 1999).

The more autonomous types of motivation (Intrinsic Motivation, Integrated and Identified Regulation) have shown to be positively related to long-term involvement in learning activities, and higher school achievement, better understanding of taught concepts, improved school satisfaction, and a lower school dropout rate (Gottfried, 1985; Ryan and Deci, 2002; Ryan, 2009; Gutman et al., 2010). Whereas, more controlled forms of motivation have been associated with students' experience of distraction, negative feelings, and lower grades (Guay et al., 2010).

Middleton showed that the more interest a student has in mathematics, the more effort the student is willing to put in, the more the student experienced the activity as enjoyable, and the more they are willing to persist in the face of difficulties (Middleton, 1995). It is likely that integrating concrete, meaningful, and purposeful physical activities such as basketball in the teaching and practicing of mathematics supports children's need for feeling autonomous and competent more than the traditional classroom teaching, and is therefore, more intrinsically motivating. The feeling of autonomy may be fostered through higher perceived purposefulness of the activities and mathematics. As such, the feeling of competence may be promoted by the involvement of less abstract and more hands-on skills and learning approaches. It is also likely that using mathematics to solve concrete tasks, as in the basketball exercises in this study, may help students to recognize and identify with the value of practicing and learning mathematics, i.e., promote the extrinsic motivation for mathematics in terms of identified regulation.

It is shown that participating in physical activity has significant benefits for children's cognition and academic education both with single bouts of physical activity (Ferris et al., 2007; Skriver et al., 2014; Hillman et al., 2019), regular physical activity (Broussard, 2004; Geertsen et al., 2016; Damsgaard et al., 2020), and high physical activity levels (Hillman et al., 2014; Donnelly et al., 2016; Marques et al., 2018).

Also, motor-enriched learning, where learning of a subject is combined with meaningful motor activities, has shown a positive effect on academic content (Beck et al., 2016). Damsgaard et al. (2020) found that motor-enriched learning improved children's academic learning (letter recognition), and the children who performed motor-enriched learning had a higher intrinsic motivation for the academic content. Teaching situations where physical activity are integrated meaningfully, may therefore influence both children's motivation and there academic performance in a positive way (Broussard, 2004; Geertsen et al., 2016; Damsgaard et al., 2020).

Our aim, with integrating mathematical tasks with concrete and physically active basketball tasks, was to make the learning activities more interesting, meaningful, play-based, and fun for the children. More specifically, we hypothesize that basketball combined with mathematics is a concrete physically active way of employing, practicing, and learning mathematics that will result in students feeling a higher degree of autonomy and competence, and is more intrinsically motivating than classroom-based mathematics.

Based on the hierarchical nature of motivation (Fortier et al., 1995; Vallerand, 2000), we further hypothesize that these positive situational experiences with mathematics will have a positive impact on the children's motivation for mathematics in general, and also in the classroom. As the basketball sessions combined with mathematical activities do not involve more cooperation and group work, we do not expect that it will have any effects on experiencing relatedness.

MATERIALS AND METHODS

Participants

In total, 757 students took part in this school-based study after obtaining written consent from parents, corresponding to 78.60% of the invited children. All students were recruited from five Danish elementary schools from within and outside the Copenhagen area. The included children came from 40 different classes at different grade levels; elementary school (1st to 3rd grade) and middle school (4th to 5th grade) (see **Table 1**). 125 participants were absent at tests days and were excluded. 207 participants were excluded from the analysis of the Academic Self-Regulation Questionnaire (SRQ-A) and 92 participants from the analysis of the Post-Experimental Intrinsic Motivation Inventory (IMI) due to incomplete data (see flow diagram, **Figure 1**). In total, the statistical analysis was made upon 459 participants for the SRQ-A questionnaire and 248 for the IMI questionnaire. At every school, the classes were randomly selected to have either BM or CON with just regular basketball

TABLE 1 | Demographics for the two intervention groups (CON, BM).

	CON			BM		
Grade level	**Total**	**ES**	**MS**	**Total**	**ES**	**MS**
Participants (n)	206	105	101	253 (248)	107 (135)	146 (113)
Age (Years)	10.40 ± 0.42	9.40 ± 0.44	11.40 ± 0.40	10.33 ± 0.39	9.30 ± 0.39	11.35 ± 0.38
Sex (% Boys)	50	51	49	54 (52)	49 (52)	58 (42)

Data reported as mean ± SD. CON, Control Group (Basketball sessions without mathematics); BM, Basketball sessions combined with Mathematics; ES, Elementary School; MS, Middle School. Baseline data made upon the included data from the SRQ-A data. SRQ-A data is based on the pre and post measurements. Note that the numbers represented in parentheses indicate the included participants in the IMI data analysis within the BM group, which is an acute measure.

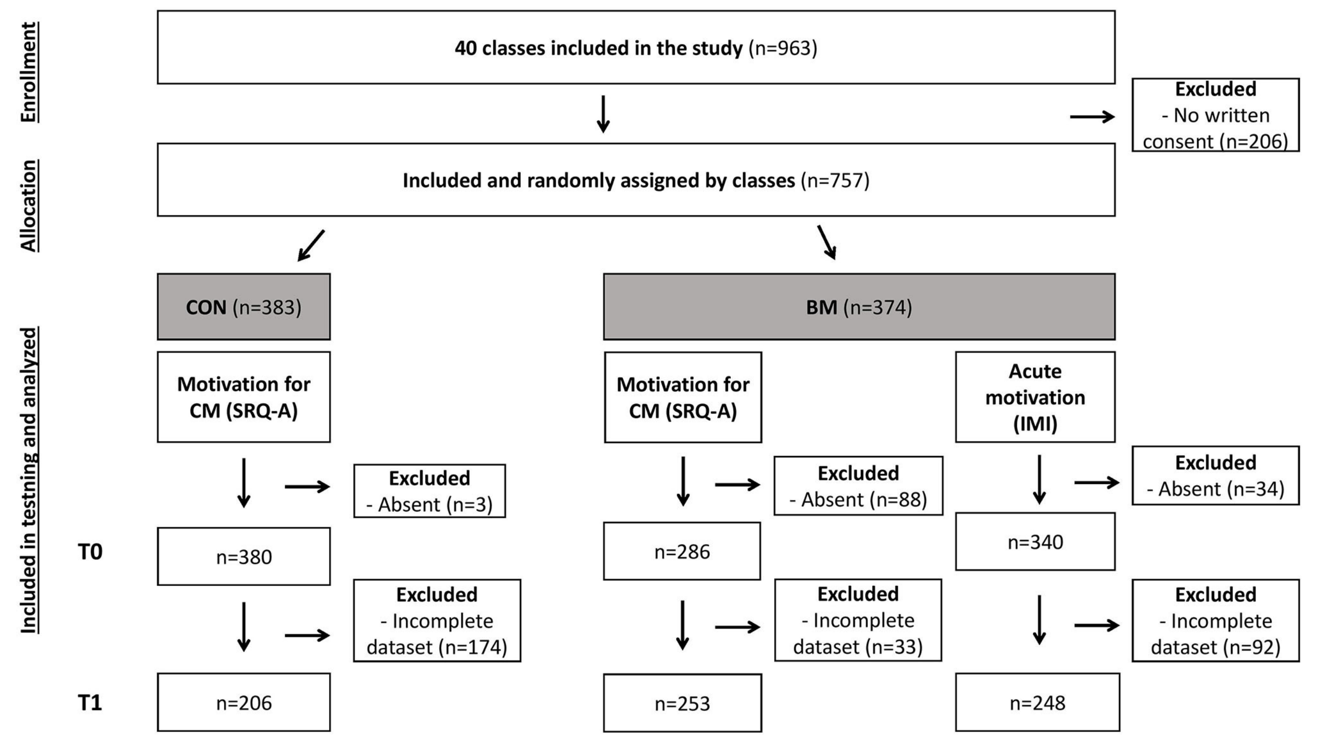

FIGURE 1 | Flow diagram. Flow diagram of the study. Seven hundred fifty-seven children were randomly assigned to either basketball sessions without mathematics (CON) or basketball sessions combined with mathematics (BM). The children performed a questionnaire (SRQ-A) about their motivation for classroom-based mathematics (CM) before (T0) and after an intervention period of 6 weeks (T1). BM also performed a motivation questionnaire (IMI) acutely after a basketball session combined with mathematics and immediately after a session of classroom-based mathematics. Only complete cases were analyzed.

training during their weekly PE lesson. The study was approved by the local Ethical Committee at the University of Copenhagen, Denmark (protocol: 504-0016/17-5000) and was carried out in accordance with the Helsinki Declaration II.

Intervention

The 374 students in the intervention group received teaching in basketball combined with mathematics built into the exercises (BM) once a week over a coherent 6 week period. Each lesson had a duration of 90 min including time to change into sportswear. That allowed ∼70 min of isolated time to focus on the exercises with basketball combined with mathematics. The control group (CON), which consisted of 383 students, received the same amount of teaching in basketball without any kind of mathematics built into the exercises. In both groups (CON and BM), the lessons were planned and ran by external trained researchers, specially recruited and educated for this project, but supported by and in cooperation with the class' normal teacher. The content of mathematics in the intervention group (BM) was adjusted to fit the actual level of each participating class by consulting their mathematics teacher and in compliance with the national curriculum. Each teaching lesson had the following structure: introduction, a warm-up-activity, exercise 1, exercise 2, exercise 3, and in the end, a finishing exercise where the teachers summarized the lesson's theme and activities with the children. During the lesson (in between the exercises), the teachers had a dialog about the elements in the practice both in relation to the task, basketball skills, and mathematics (only in the BM group). The mathematical theme was meaningfully built into the exercises. The children, for example, were tasked with collecting and calculating mathematical information through different basketball exercises. Other exercises were more play-based, where the children had to perform mathematics (multiplication, addition, etc.) and basketball skills to win games. For a more detailed overview of mathematical content and basketball skills, see **Figure 2** and the website: www.basketballmathematics.org. The design setup was a mix between different exercises, where some exercises were more motor-enriched and some were more focussing on high loaded cardiovascular.

In structuring the transitions between the lessons, transfer and recognition were key elements. Recognition refers to how the children should easily recognize the game and the structure to reduce misunderstandings and confusion, and therefore, specific exercises were reused. Transfer refers to the aspect of reusing exercises and lesson structure, but introducing a shift in the content, for example, from lay-up to shooting from a distance. Similarly, the mathematics could change from addition to subtraction. From a pedagogical perspective, the reuse of games made it easy to change the content of the exercises slightly and still keep the children's attention, and thereby, support them in understanding the structure of the exercise.

Test Procedures

Data about age and sex were collected prior to the baseline measures for all children. For the BM group, measures of acute intrinsic motivation (IMI) and the satisfaction of the basic psychological need for autonomy and competence during the two ways of teaching mathematics were collected immediately after one lesson with basketball combined with mathematics, and immediately after one lecture of classroom-based mathematics (CM). For the two groups (CON, BM), measures of the children's motivation for CM were collected at baseline T0 and were post-evaluated after the 6 weeks of intervention period (T2).

MEASURES

Post-Experimental Intrinsic Motivation Inventory (IMI)

The Post-Experimental Intrinsic Motivation Inventory (IMI) (McAuley et al., 1989) was used to measure acute intrinsic motivation and experiences of competence and autonomy for the BM group. All participating school classes in BM completed the questionnaire in lessons 2–5 at the end of a normal CM lesson during the intervention (see **Figure 2**), and also, after one session of basketball combined with mathematics.

IMI measures participants' subjective experience while performing an activity in an experiment, and has been found to be a valid self-reported measure of intrinsic motivation (McAuley et al., 1989; Markland and Hardy, 1997). The scale has previously been used in other studies on the motivational effect of integrating physical and learning activities in primary schools (Vazou et al., 2012).

As a measure of intrinsic motivation, four items from the Interest/Enjoyment scale were used. The used items were: "I really enjoyed the activities"; "The activities were fun"; "I thought it was boring" [Reverse question (R)]; "I thought the activities were interesting."

To measure the children's experience of autonomy, three items from the Perceived Choice subscale were used: "I believe I had some choice about doing this activity"; "I did this activity because I wanted to"; "I did this activity because I had to" (R).

To measure the children's experience of competence, the following items from the Perceived Competence subscale were used; "I think I am pretty good at this activity"; "I am satisfied with my performance at this task"; "This was an activity that I couldn't do very well" (R).

Items were translated into Danish using a translation-backtranslation process (Streiner et al., 2015). Because the scales were used on children, the original 7-point response-scale was converted to a 4-point scale (1; not true at all, 2; Only slightly true, 3; almost true, 4: True). The investigator read the questions aloud for the children one by one. As an introduction to the specific questions, children were asked how they experienced the lesson they had just taken.

Motivation for Classroom-Mathematics/CM (SRQ-A)

For all participating school classes in both CON and BM, children's motivation for mathematics was measured using the Academic Self-Regulation Questionnaire (SRQ-A). The questionnaire was filled in during a CM lesson 1 week before the 6 weeks intervention (T0) and 1 week after the last lesson of

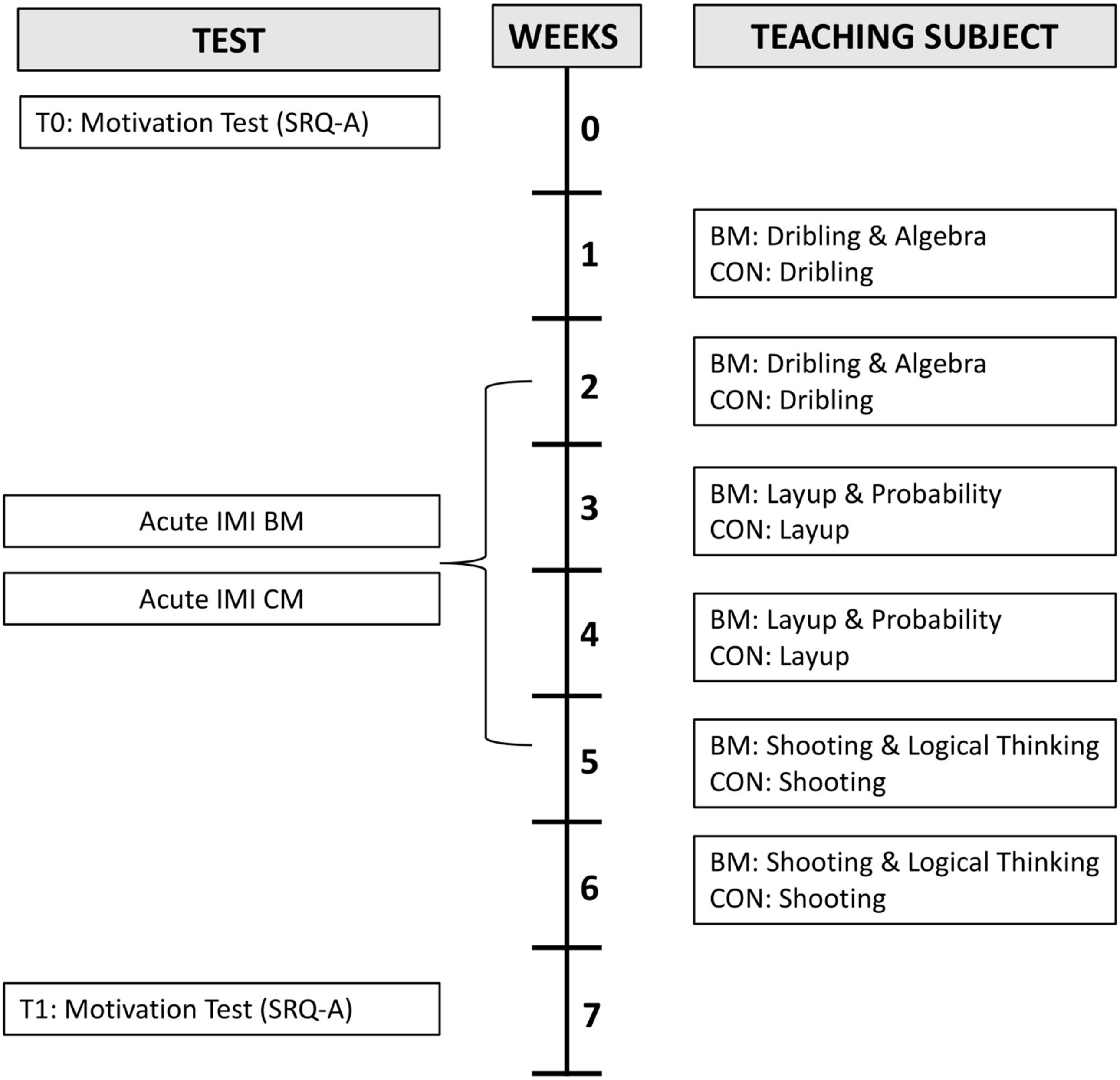

FIGURE 2 | Intervention overview. Two groups (BM: Basketball combined with Mathematics and CON: Basketball without mathematics) were tested before (T0) and after (T1) an intervention period of 6 weeks with an SRQ-A motivation questionnaire. Within the BM-group, the children performed acutely motivation questionnaire (IMI) in basketball sessions combined with mathematics (Acute BM), and in classroom-based sessions with mathematics (Acute CM) randomly in week 2–5. The figure also shows the different teaching themes in CON and BM.

the intervention period (T1). The questionnaire was completed together with the children's own mathematics teacher.

The SRQ-A is a widely used SDT-based domain-specific 32-item self-report instrument, developed for measuring the degree of different types of motivation for doing schoolwork among children in the late primary and lower secondary school. The SRQ-A uses scales to measure both extrinsic types of motivation (external regulation, introjected regulation, and identified regulation) and intrinsic motivation. Items are organized in four main topics: (1) "Why do I do my homework?," (2) "Why do I work on my classwork?," (3) "Why do I try to answer hard questions in class?," and (4) "Why do I try to do well in mathematics?." In the present study, the homework domain was not included, as regular homework is not common at the Danish grade levels presently studied, resulting in a questionnaire of 24 items.

The questions are answered on a four-point Likert scale (1 = Not at all true, 2 = Not very true, 3 = Sort of true, and 4

= Very true) and summed up to calculate scores for the five types of motivation across the four areas. The SRQ-A was originally validated by Ryan and Connell (1989) for students in Grades 3–6 (approximate age: 8–12). The SRQ-A is widely used and has shown across studies, samples, and contexts to be a moderately reliable measure, which is stable across subscales (Burton et al., 2006; Dettweiler et al., 2015). Following a translation/back-translation process (Streiner et al., 2014), the instrument was translated from English into Danish.

Statistical Analysis

Psychometric Qualities of the Included Measures

The validity of the SRQ-A and IMI scales were estimated by conducting two exploratory structural equation modeling (ESEM) analysis adjusting for clustering on grade level and school, in Mplus (Muthén and Muthén, 2012). For IMI, measures collected from the intervention group at BM and CM were evaluated. For SRQ-A baseline, measures for the total sample were evaluated. Loadings and cross loadings and model fit were inspected. Loadings >0.3 on intended factor and <0.3 on unintended factors were considered acceptable. Criteria used to indicate a good model fit were: Chi2/df < 5.00, CFI > 0.95, TLI > 0.95, RMSEA < 0.06 (Hu and Bentler, 1999). To estimate the internal reliability of the psychometric scales, Cronbach's alpha values were calculated with values above 0.6 indicating an acceptable internal consistency of the items (Ponterotto and Ruckdeschel, 2007).

Analysis of Intervention Efficacy

The statistical analyses of intervention efficacy were performed in R Studio (R Core Team, Vienna, Austria).

Data from the acute motivation questionnaire (IMI) were analyzed for the intervention group using paired *t*-test to identify possible differences in means.

Data from the SRQ-A questionnaire were analyzed using a linear mixed model with group-time interaction as fixed effects, using the R-packages lme4 (Bates et al., 2017). The data was analyzed for group x time interactions with CON and BM as groups and time were T0 and T1. To account for the cluster structure and the repeated measures in the data, "subjects," "school," and "grade-level" were added as fixed effects. Ratio Tests were used to reveal group x time interactions effects for differences before and after the 6 weeks of intervention. Subsequently, if the test for interaction was significant, pairwise comparisons between delta values were used to characterize the interaction effect. To reduce the problem of multiple testing, only relevant model-based specified comparisons were performed including the comparisons of interest (time and group differences) using the *emmeans* R-package (https://CRAN.R-project.org/package=emmeans).

The linear mixed model was chosen as a statistical tool, due to the possibilities in the model when working with repeated observations. The model can be used when dealing with missing data, treating continuous and categorical responses as well as unprincipled methods of modeling heteroskedasticity and non-spherical error variance (for either participant or item) (Baayen et al., 2008). The linear mixed effect models have addressed each of these concerns, and offer, thereby, a better approach than univariate ANOVA.

For all tests, a significance level of 0.05 was applied. Data are reported as means ± SD unless otherwise stated.

RESULTS

Psychometric Properties of the Motivation Measures

For measures taken within the intervention group for Acute Intrinsic Motivation (IMI) at both Basketball combined with mathematics (BM) and Classroom-based mathematics (CM), ESEM analysis of the IMI with distinct factors for perceived autonomy, competence, and intrinsic motivation showed acceptable high loadings on the intended factors and no issues with cross loading. The model fit met the criteria for a good model fit. For BM, RMSEA = 0.070 (90% CI 0.041–0.100); CFI = 0.985; TLI = 0.963. For CM, RMSEA = 0.028 (90% CI 0.001–0.066); CFI = 0.999 and TLI = 0.996. Results depicting the factor loadings of items of the IMI can be seen in **Appendix 1**.

ESEM analysis of the SRQ-A showed some minor issues with one low item loading in identified regulation and one low item loading on external regulation as well as some cross loading from external regulation to introjected regulation. However, the model fit indices met criteria for a good model fit [RMSEA = 0.048 (90% CI 0.041–0.055); CFI = 0.933; TLI = 0.900]. It was decided to use the original factor structure in the further analysis in this present study since the original factor structure has been validated and used in many studies, the model fit was good and finally, that the Cronbach's alpha values were acceptable. Results depicting the factor loadings of items of the SRQ-A can be seen in **Appendix 2**.

Both the SRQ-a scales and the IMI scales all had Cronbach's alpha values above 0.6.

Acute Intrinsic Motivation (IMI) Within BM

The children in the intervention group participating in basketball sessions combined with mathematics (BM) had significantly higher acute levels of perceived autonomy (+14.24%, $p < 0.0001$), competencies (+6.33%, $p < 0.0001$), and intrinsic motivation (+16.09%, $p < 0.0001$) during basketball sessions combined with mathematics compared to when having classroom mathematics (CM), see **Figure 3**, **Table 2**.

Subgroup analyses based on grade level showed significantly higher levels for both elementary school (ES) and middle school (MS) for basketball sessions combined with mathematics compared to CM in perceived autonomy (ES: +11.67%, $p = 0.002$; MS: +14.51%, $p < 0.0001$) and intrinsic motivation (ES: +13.23%, $p < 0.0001$; MS: +17.12%, $p < 0.0001$). However, only children in middle school experienced significantly higher levels of competencies (+17.12%, $p < 0.0001$). No other significant differences were found between age groups, sex, or other subgroups.

Motivation for Classroom-Based Mathematics (SRQ-A)

Likelihood Ratio Test showed a global significant interaction between time and group ($p = 0.002$) for intrinsic motivation for

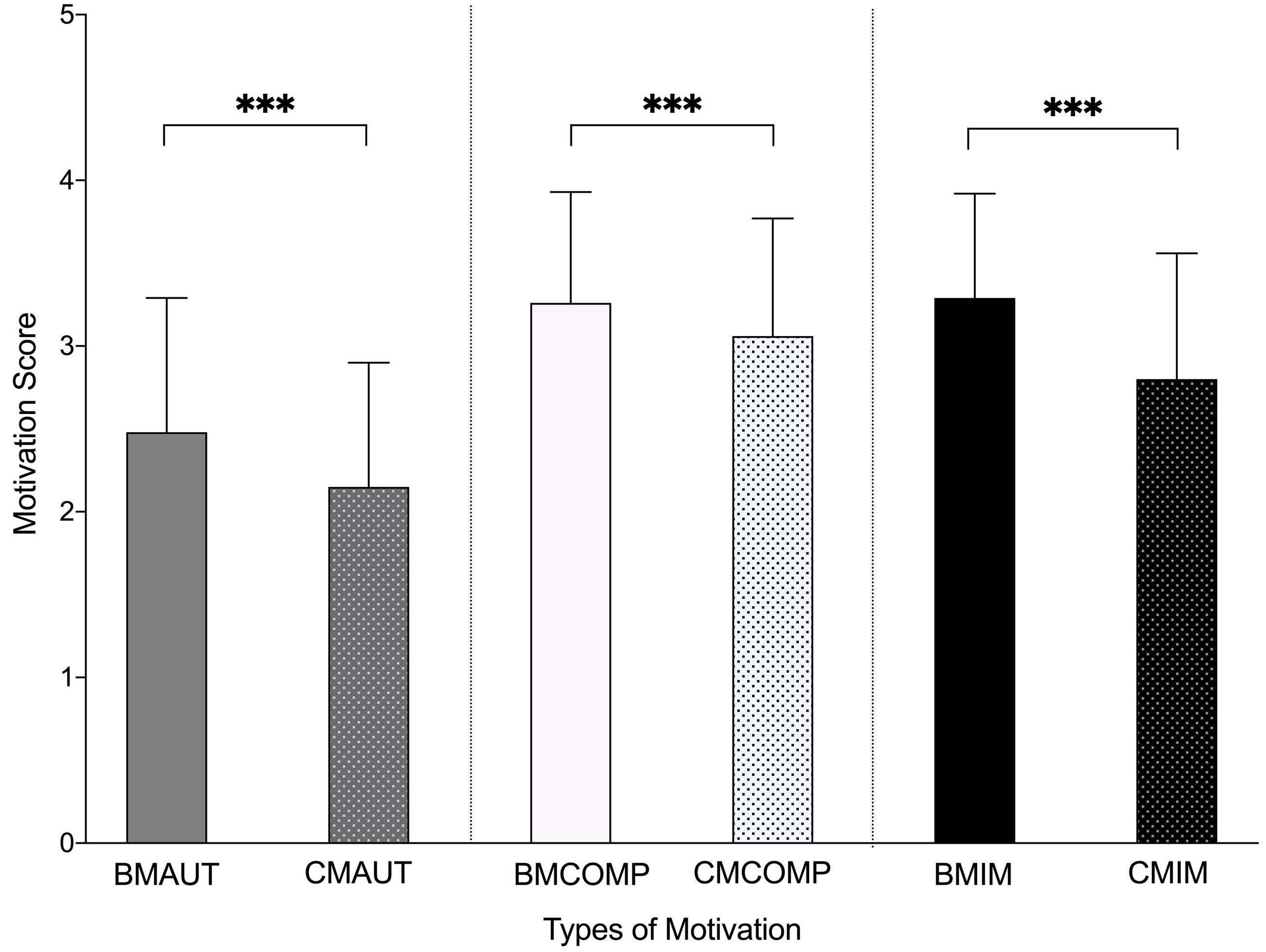

FIGURE 3 | Acutely Motivation (IMI) for the Intervention Group (BM). Acutely IMI measures for BM (Basketball sessions combined with mathematics). Motivation for sessions with basketball combined with mathematics (BM) were compared with motivation for classroom-based mathematics (CM) for the three different motivation types; autonomy (AUT), competencies (COMP), and intrinsic motivation (IM), *Indicates a significant difference between the two teaching methods (basketball combined with mathematics and classroom-based mathematics).

TABLE 2 | Acute Motivation (IMI) for the intervention group, BM, for sessions with Basketball combined with Mathematics (BM), and for Classroom-based Mathematics (CM).

Motivation measures	BMAUT	CMAUT	% DIFF	BMCOMP	CMCOMP	% DIFF	BMIM	CMIM	% DIFF
BM (*n* = 248)	2.48 ± 0.81	2.15 ± 0.75*	+14.25	3.26 ± 0.67	3.06 ± 0.71*	+6.33	3.29 ± 0.63	2.80 ± 0.76*	+16.09

*Data reported as mean ± SD and percentage difference (% diff). Motivation measures are reported as BMAUT (Motivational autonomy for Basketball sessions combined with Mathematics/BM), BMCOMP (Motivational competencies for BM), BMIM (Intrinsic motivation for BM), CMAUT (Motivational autonomy for Classroom-based Mathematics/CM), CMCOMP (Motivational competencies for CM), CMIM (Intrinsic motivation for CM). *Indicates a significant difference between the same motivation factor, but in different teaching approaches (BM and CM).*

mathematics. Further analyses showed a significant decrease in means of intrinsic motivation from T0 to T1 for CON [-9.38%, $p < 0.001$ but not for BM (+0.39%, $p = 0.98$)], see **Figure 4**, **Table 3**. A significant interaction was found for BM compared to CON from T0–T1 ($p = 0.006$) for intrinsic motivation, meaning that BM had a more positive influence on children's intrinsic motivation for classroom-based mathematics compared to CON. No differences were seen between the intervention and control groups in changes in any of the extrinsic types of motivation for mathematics, where both groups showed insignificant declines.

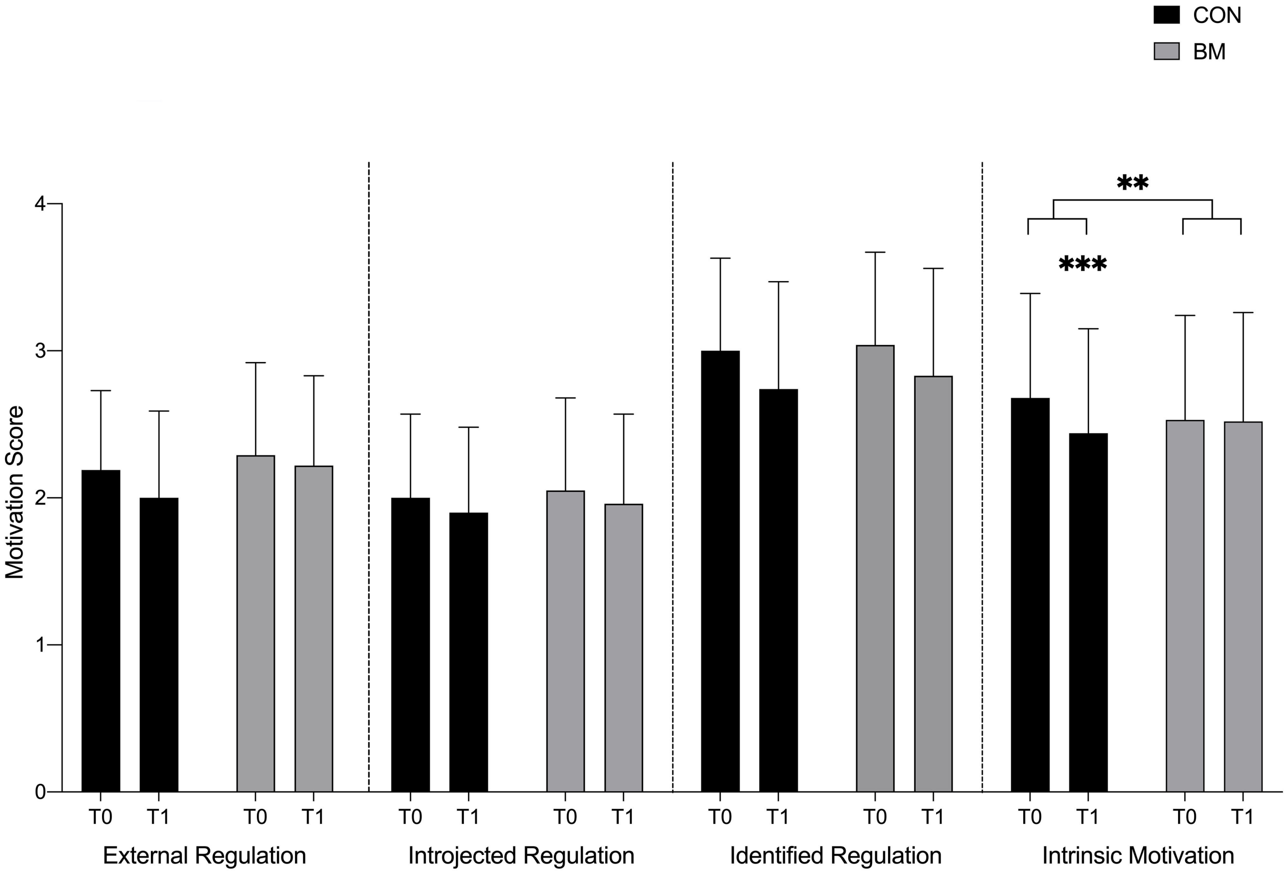

FIGURE 4 | Motivation (SRQ-A) for Classroom-based Mathematics for the two Intervention Groups (CON, BM) at T0 and T1. Motivation for classroom-based mathematics before (T0) the 6 weeks intervention period and after (T1) for the four motivation types; External Regulation, Introjected Regulation, Identified Regulation, and Intrinsic Motivation. A significant decrease in intrinsic motivation ($p < 0.001$, ***) was seen from T0 to T1 for CON, and a significant interaction was found for BM compared to CON from T0–T1 ($p = 0.006$, **) for intrinsic motivation.

TABLE 3 | Motivation score from SRQ-A questionnaire from T0 and T1 for classroom-based mathematics for the two intervention groups (CON and BM).

Motivation measures	External regulation			Introjected regulation			Identified regulation			Intrinsic motivation		
	T0	T1	% Diff	T0	T1	% Diff	T0	T1	% Diff	T0	T1	% Diff
CON	2.19 ± 0.54	2.0 ± 0.59	−9.07	2.00 ± 0.57	1.90 ± 0.58	−5.13	3.0 ± 0.63	2.74 ± 0.73	−9.06	2.68 ± 0.71	2.44 ± 0.71$^{*\#}$	−9.38
BM	2.29 ± 0.63	2.22 ± 0.61	−3.10	2.05 ± 0.63	1.96 ± 0.61	−4.49	3.04 ± 0.63	2.83 ± 0.73	−7.16	2.53 ± 0.72	2.52 ± 0.74	−0.39

*Data reported as means ± SD and percentage difference (% diff). Motivation score for classroom-based mathematics for control group (CON) and intervention group (BM). Motivation is divided into External Regulation, Introjected Regulation, Identified Regulation, and Intrinsic motivation, and were measured before (T0) and after (T1) the 6 weeks intervention period. *Indicates a significant difference between the same motivation factor both in different teaching approach (Basketball sessions combined with mathematics and classroom-based mathematics) #Indicates a significant interaction from T0 to T1 between CON and BM.*

DISCUSSION

Experiences of Competence, Autonomy, and Intrinsic Motivation During Sessions of Basketball Combined With Mathematics Compared to Usual Classroom-Based Mathematics

In the present study, it is shown that combining and integrating mathematics into basketball in a school setting were associated with higher acute levels of experienced autonomy, competence, and intrinsic motivation than classroom-based mathematics within the BM group. Intrinsic motivation for a learning activity reflects that children enjoy the activities and experience more engagement due to this enjoyment (Ryan and Deci, 2000). As described in SDT, maintaining intrinsic motivation for an activity is dependent on the participants experiencing autonomy, competence, and relatedness during the activity (Deci and Ryan, 1985; Reis et al., 2000). Using mathematics in more concrete tasks, such as the basketball exercises in this present study, might have made mathematics seem more relevant to the pupils, which, in other studies, has shown to increase student's perceived autonomy (Su and Reeve, 2011), intrinsic motivation for, and involvement in the learning activities (Weaver and Cottrell, 1988; Sass, 1989; Frymier and Shulman, 1995; Simons et al., 2003; Kember et al., 2008). This is supported theoretically by the self-determination theory (Deci and Ryan, 1985) where relevance is described as important to the internalization process, promoting a more autonomous motivation for the activity. It might also be that a more concrete practical use of mathematics gives children more experiences of competence.

These findings are in line with other studies where physical activity is integrated in the learning situations (Vazou et al., 2012; Vazou and Smiley-Oyen, 2014; Damsgaard et al., 2020). Damsgaard et al. showed that integrating movement in the teaching situation increased children's learning (letter recognition) but also increased the children's intrinsic motivation (Damsgaard et al., 2020). In the present study, we have not assessed academic performance as an outcome, however, it could be relevant to investigate whether increased motivation in the BM group positively affects academic performance.

Effect of the Intervention on Children's Motivation Compared to the Control Situation

The results from the SRQ-A questionnaire implied that having basketball combined with mathematics (BM) sessions can help maintain children's intrinsic motivation for classroom-based mathematics compared to a control situation without BM (CON).

Intrinsic motivation for a subject has shown to be of importance to academic achievement (Gottfried, 1985; Ryan and Deci, 2002; Singh et al., 2002; Ryan, 2009; Gutman et al., 2010). Furthermore, it can be argued that children's enjoyment of mathematics and of classroom activities is an important goal in itself. The potential supplementary function of why basketball combined with mathematics is motivating for mathematics, in general, is in accordance with the hierarchical nature of motivation, which proposes that motivation from one teaching situation can lead to an increase in general school motivation (Vallerand, 2000).

However, no differences were seen between the intervention group and the control group's development in extrinsic types of motivation for mathematics. It was hypothesized that having concrete experiences with the usefulness of mathematics in solving concrete tasks in BM would also increase the students' Extrinsic Motivation Identified. However, this hypothesis could not be confirmed by the data.

Furthermore, no differences were seen in the two most controlled forms of motivation, introjected and external regulation, which can be seen as a quality of the intervention, as these types of motivations often have a negative impact on long term enjoyment, engagement, and continuation with the activities (Guay et al., 2010).

Practical Recommendations for Basketball Combined With Mathematics and Perspectives

This concept is developed in a Danish school context with the perspective of what is possible. The model might give new ideas for the development of other teaching concepts and, therefore, some reflections on the basis of basketball combined with mathematics (further details are found in Wienecke and Damsgaard, 2020). The teaching setup of having this type of teaching within the physical education classes once a week is suitable to the minimum standard of all public schools in Denmark. The duration of 6 weeks fits in between school vacations so the course can be taken in one coherent period at several different times during the school year, which makes this model practically feasible in a school setting. Facilities at schools varies but the idea behind this intervention, is that you only need two baskets pr. class and one ball for every four children. These minimalistic requirements make it easy for all public schools to use the activities. Scaling up or reconfiguration is easy both in terms of lesson frequency, intensity, and in relation to the structure of the activities.

The structure of the activities is based on some important concepts to create a good learning environment such as togetherness, play and equal focus on developing skills in both basketball and math. The children are always assigned into groups of two or more. This can create a feeling of solving the assignments together and avoid loneliness and incompetence when assignments are found difficult and hopefully, get the common joy of that. It is equally important to develop skills within basketball and as well as in math. The underlying intention is that the children should have the feeling of becoming better, for example, at scoring points and/or solving the math assignments. Implicit in the assignments is that the children have to think, reflect, talk, and use the language of math which can help the children in verbalizing the math terminology and become confident with it.

The assignments are usually starting out in the easiest way and then after the first or second round the assignments are adjusted. For example, shooting drills begin close to the basket so the children hit the basket as often as possible, and then later, the distance increases and the difficulty of hitting the basket will likewise be more challenged. This is the same for the math part (i.e., easy start and then more difficult).

Competition is an element in basketball combined with mathematics but never as a traditional five on five game. The children often compete indirectly. Indirect competition could, for example, be reflected in a situation where the children have to finish first within an assignment but during the competition, they do not always know how far the others are. This practical recommendation can facilitate that the children focus on their own performance instead of on the competitors. The play element is very important. The children should have the feeling of being included in the task and also have the possibility to solve the assignments in their own way or develop their own ideas within the frame of the lesson.

The finding that sessions with basketball combined with mathematics (BM) has a positive effect on children's general intrinsic motivation for classroom-based mathematics is remarkable and supports initiatives where integrating physically active games and play with curriculum based academic tasks are used as a supplement to the more traditional classroom teaching. In this study, the combination of basketball and mathematics was chosen, but physically active play-based teaching methods could be combined with other theoretical themes such as language, biology, physics, etc.

For further exploration of the effects of basketball sessions combined with mathematics, it would be interesting to investigate both short- and long-term effects on the children's mathematical performance before and after a BM intervention.

Strengths and Limitations of the Study

The present study is unique in its study design and sample size. The intervention intensity (i.e., once a week of basketball combined with mathematics) can easily be organized in the public school because it only requires the allocation of physical education classes. The BM does not require an extensive teaching material but only two baskets and some basketballs. As described above, only a few studies have investigated the effects of integrating physical activity and academic learning in a meaningful way as in this study. A limitation of the study is that only a few acute motivation measures were collected (see **Figure 2**). Furthermore, the intervention group, BM, had external trained researchers to carry through the project, which may have led to differences in the teaching capacity and learning environment. Due to the large number of school classes, trained researchers and teachers involved in this present study the bias should be small. Furthermore, the analysis was adjusted for clustering on school and grade level. Finally, it could have been interesting to measure the children's academic achievement, however, this was beyond the purpose of this study.

CONCLUSIONS

This study shows that basketball combined with mathematics is an intrinsically motivating way to practice mathematics, which also has a positive influence on children's more general intrinsic motivation for mathematics in the classroom.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by the Local Ethical Committee at UCPH. Written informed consent to participate in this study was provided by the participants legal guardian/next of kin.

AUTHOR CONTRIBUTIONS

JW, JH, and GN designed the experiment. JH and KM collected the data. LD conducted the required data analysis and the first draft of the manuscript. All authors contributed to drafting the manuscript and approved the final version of the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpsyg.2021.636578/full#supplementary-material

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Negative Effects of Embodiment in a Visuo-Spatial Working Memory Task in Children, Young Adults, and Older Adults

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Studies examining the effect of embodied cognition have shown that linking one's body movements to a cognitive task can enhance performance. The current study investigated whether concurrent walking while encoding or recalling spatial information improves working memory performance, and whether 10-year-old children, young adults, or older adults (M_{age} = 72 years) are affected differently by embodiment. The goal of the Spatial Memory Task was to encode and recall sequences of increasing length by reproducing positions of target fields in the correct order. The nine targets were positioned in a random configuration on a large square carpet (2.5 m × 2.5 m). During encoding and recall, participants either did not move, or they walked into the target fields. In a within-subjects design, all possible combinations of encoding and recall conditions were tested in counterbalanced order. Contrary to our predictions, moving particularly impaired encoding, but also recall. These negative effects were present in all age groups, but older adults' memory was hampered even more strongly by walking during encoding and recall. Our results indicate that embodiment may not help people to memorize spatial information, but can create a dual-task situation instead.

Keywords: embodiment, memory, cognition, spatial information, age comparison

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INTRODUCTION

The human brain can store almost unlimited amounts of information in its episodic memory. Many of these memories contain information about the environment and the position of one's own body (e.g., when trying to remember where you bought a shirt, information about the store and how you went there are reactivated). Perceiving and encoding multimodal information leads to stronger memories compared to information that was encoded by only one modality (Jahn and Engelkamp, 2003; Feyereisen, 2009). This phenomenon has also been shown in the context of the intersensory-redundancy hypothesis (Bahrick and Lickliter, 2014). This hypothesis states that if the same information is perceived by more than one modality (e.g., seeing a speaker's mouth while hearing the sound of his/her voice), amodal information like speech rhythm can be perceived more easily, and is more likely to be encoded (intersensory facilitation). Bahrick and Lickliter (2014) emphasize the role that intersensory redundancy plays in the development of selective attention in infancy and early childhood.

Self-performed tasks are multimodal, meaning that multiple sensory systems are involved during encoding (Bäckman et al., 1986). One of these modalities is proprioception, which provides information about one's own body movements. In our example of purchasing a shirt, this means that you will have a stronger memory of it if you tried it on and felt its material and shape rather than just looked at it. Sensorimotor information can improve memory even more when the respective body movement is meaningfully related to the cognitive processes (Bäckman et al., 1986; Mavilidi et al., 2016; Hainselin et al., 2017; Skulmowski and Rey, 2018). The embodied cognition framework (Barsalou, 2008; Glenberg, 2010) claims that sensorimotor experiences and bodily states are essentially involved in higher cognitive processes. It postulates that the human mind is grounded in mechanisms that have evolved from interaction with the environment, including sensory processing and motor control (Wilson, 2002). According to this framework, sensory processes not only contribute to creating memories, but are also reactivated during recall to simulate past experiences (Barsalou, 1999). These simulations are rich in detail because of their multimodal structure, since they encompass relevant motor and mental states that are part of the original experience (Dijkstra and Zwaan, 2014). The embodied cognition framework has attracted a lot of research attention in the last years (see reviews by Beilock, 2008; Kiefer and Trumpp, 2012; Loeffler et al., 2016; Krüger and Ebersbach, 2018). Studies on the mirror neuron system also support an embodied view on cognition (Hauk and Pulvermüller, 2004; Tettamanti et al., 2005). However, the approach has also been criticized for not being clearly distinguishable from more traditional cognitive accounts (Mahon and Caramazza, 2008; Caramazza et al., 2014).

An interesting aspect of embodiment effects relates to their developmental trajectory: Does embodiment exert similar effects across the lifespan, or are there age-related changes in its influence on cognition? Recent studies indicated that young children may profit more from embodiment than older children or adults do (Link et al., 2013; Hainselin et al., 2017; Schaefer, 2019). This is in line with Piaget's theory of cognitive development (Piaget, 1975), emphasizing that physical experiences are substantial in the very early stages of the lifespan and become less important with increasing age. Pouw et al. (2014) also expected larger effects of embodiment in children, as learners disembed their mental activity from the environment over time.

In a lifespan approach of embodied cognition, Loeffler et al. (2016) argued that embodied cognition effects are driven by two underlying processes, either by "new" associations (e.g., learning how shape influences the movements of new objects) or by "reactivated" associations (e.g., remembering the flight quality of an American football that you have experienced before). "New" associations imply that the sensorimotor information that is generated during action (e.g., when interacting with an object) supports the generation of conceptual knowledge, while "reactivated" associations refer to how previous experiences influence the encoding of new information (e.g., anticipating the landing location of an American football on the basis of its flight qualities). Loeffler et al. (2016) stated that children may be more dependent on new associations compared to older adults, and are therefore more strongly affected by embodiment effects involving the formation of those associations. On the other hand, older adults may profit more from the reactivation of previously experienced associations, because their accumulated life experiences increase the likelihood of encountering situations that are similar to past experiences. A recent study by Wermelinger et al. (2019) on action perception and action production also adopted a lifespan approach. Older adults were more successful in predicting the consequences of unfamiliar actions compared to younger individuals, which may be related to their accumulation of motor experience with different actions over the lifespan.

While Loeffler et al. (2016) emphasized the benefits that embodiment may have for older adults, Costello and Bloesch (2017) argued that older adults may be generally less embodied than younger adults, because they rely more on visual processing and less on bodily factors (kinesthetic, tactile, proprioceptive). Furthermore, there is a rich literature on older adults' increased likelihood to show more pronounced performance deteriorations in cognitive-motor dual-task situations (for reviews, see Woollacott and Shumway-Cook, 2002; Al-Yahya et al., 2011; Schaefer, 2014). In part, this may be due to age-related declines in sensory and motor abilities, increasing the need to invest mental resources like attention into the motor domain. According to cognitive load theory (see Sweller et al., 1998, 2019; Brünken et al., 2003), full-body movements that increase cognitive load may reduce the performance of concurrent cognitive tasks, for example by interfering with memory encoding strategies (Amico and Schaefer, 2020). In contrast, the embodied cognition literature would expect meaningful full-body movements to decrease cognitive load, e.g., by "offloading" cognitive content to the environment (Wilson, 2002). The current study investigates embodiment effects over the lifespan, by comparing children to young and older adults, with the aim to disentangle embodiment and dual-task effects.

Recent studies have shown that embodied training can effectively improve cognitive processes of learning and memory in children, adults, and older adults (Dijkstra et al., 2007; Fischer et al., 2011; Link et al., 2013; Moreau et al., 2015). In this context, Kontra et al. (2015) could demonstrate that an embodied science teaching improves memory performance. College students who physically experienced angular momentum by spinning wheels themselves (embodied condition) answered more questions correctly in a later quiz about angular momentum and torque compared to a group of observers who were not exposed to any motor experience themselves. Furthermore, the significant improvement in learning correlated with the activation of sensorimotor brain regions when students reasoned about angular momentum. This relates well to Barsalou's (1999) concept of embodied simulations, which states that sensory processes are reactivated during recall to simulate the past event. In addition, Lindgren et al. (2016) were able to show the positive effects of embodiment when teaching students aged 12–13 years about gravity and planetary motion. They used an immersive and interactive simulation in which students moved an asteroid using their own body. The control group used a desktop version of the same simulation. The embodied interactive simulation improved the learning gains, engagement, and attitude of students toward science.

In another study, Dijkstra et al. (2007) were able to show that young and older adults can profit from embodiment. Participants had to recall eight memories in combination with either one congruent or one incongruent body posture (an example of a congruent posture would be to lie down while remembering one's last dental treatment). Both age groups recollected more memories associated with a congruent body posture in a free recall test 2 weeks later. The positive effect of congruent body movements and self-performed tasks over non-movement conditions is also effective when memorizing vocabulary and phrases (see Jahn and Engelkamp, 2003; Manzi and Nigro, 2008; Feyereisen, 2009).

The close relationship between spatial cognition and motor processes has been shown for numerous cognitive tasks including mental rotation (Amorim et al., 2006), spatial visualization (Chu and Kita, 2011), and mental imagery (Frick et al., 2009). Krüger et al. (2014) asked young adults in a mental rotation task whether two simultaneously presented stimuli were identical. The images either showed simple cubes, cubes with colored ends, cubes with body parts in anatomically possible locations, or cubes with body parts in anatomically impossible locations. Participants were fastest and made fewer errors in the possible-body condition, and were slowest and made most errors in the impossible-body condition. The authors concluded that embodiment is an inflexible mechanism that cannot be willingly turned off, such that it may even impede performance under certain circumstances.

Meaningful body movements like gestures may be able to reduce cognitive load and thus improve performance in learning lists of items (Goldin-Meadow et al., 2001), in mental rotation tasks (Ehrlich et al., 2006), and in navigation tasks (So et al., 2014). So et al. (2015) were able to show that gestures are even more effective than spatial language is during rehearsal of spatial information. In their study, young adults learned routes that contained lines with varying directions (vertical, horizontal, diagonal, etc.). In a between-subjects design, participants remembered more routes correctly in conditions in which they were allowed or explicitly encouraged to use gestures during rehearsal as compared to conditions in which they were allowed or encouraged to use spatial language, or conditions in which gestures, language, or both strategies were prohibited.

A recent study by Schaefer (2019) on embodied cognition effects used full-body movements in spatial working memory. She tested 7- and 9-year-old children in a spatial version of a 2-back task and young adults in a spatial 3-back task. Stimuli were presented in a row of nine adjacent fields depicted on the floor. Target fields turned red. The task instruction was to indicate whenever a stimulus was presented at the same position as the stimulus presented n positions before (2-back or 3-back, depending on the age group) by saying "tap." In a within-subjects design, participants either stepped into the target fields while working on the n-back task (embodied condition) or stood still (control condition). The results showed performance improvements in the embodied condition for 7-year-olds, but not for 9-year-olds and young adults. The author argued that the use of more efficient memory strategies in older children and adults may have blurred the beneficial effects of embodiment in the older groups.

Amico and Schaefer (2021) recently attempted to replicate the positive effect of embodiment using a verbal memory task. Children, teenagers, and young adults participated in the study. In a within-subjects design, they were asked to encode strings of numbers, which were either presented while sitting, or with the instruction to move to the corresponding position in space (numbered gymnastic mats). Contrary to predictions, embodiment did not increase recall performances, but led to inferior performances as compared to the sitting condition. Only the youngest age group (8-year-olds) did not show performance differences between the sitting and embodied condition. The authors proposed that the need to move to the respective location, in addition to the interference created by a group setting, may have led to the findings. These assumptions were supported by the second experiment, in which 7-year-olds and young adults were tested in individual test sessions. In this case, there were no costs, but also no benefits in the embodied condition compared to a standing condition. In addition, target numbers were always presented verbally, visually, and as a spatial location, leaving participants with numerous potential strategies to encode the number sequence (i.e., verbal rehearsal or the encoding of spatial positions). A stronger and more exclusive reliance on spatial information ought to increase the chances of finding positive effects of embodiment on spatial memory.

The current study aims to further contribute to the understanding of embodiment in spatial memory, since previous studies could not consistently show positive effects of embodiment. The current literature about embodiment in spatial memory has mainly focused on episodic memory tasks using small-scale movements like gestures. In addition, only very few studies were able to contribute to a lifespan perspective on embodiment. Therefore, the current study investigates possible effects of embodiment in children, young adults, and older adults in a spatial working memory task using full-body movements. Spatial memory develops rapidly from infancy to the preschool years, reaches a plateau in young adulthood, and declines again in older adulthood. At the age of 10 years, children have achieved an advanced hierarchical coding system that continues to develop until young adulthood (Newcombe and Sluzenski, 2004; Newcombe and Learmonth, 2005). Young adults show higher spatial and verbal working memory performance compared to children and older adults (Jenkins et al., 1999). In older adults, starting at the age of around 60 years, spatial memory progressively declines with increasing age (Hedden and Gabrieli, 2004; Colombo et al., 2017; Lester et al., 2017). We tested children at the age of 10 because they were already able to follow the instructions of the tasks, while still differing from young adults in their spatial memory capacity (Zald and Iacono, 1998). Older adults beyond the age of 60 should be affected by age-related declines in cognitive performance.

To measure spatial memory performance in an embodied setting, we decided to use a customized version of a standardized psychological test, namely the Corsi Block-Tapping Task (CBT), a well-known test to measure memory span (Corsi, 1972). The CBT consists of nine small blocks positioned in a standard random configuration on a board. The participant's task is to memorize and recall sequences of blocks that the test administrator has pointed at. The sequences increase in length over the trials until the participant fails to correctly recall the sequences on several consecutive trials. A study by Piccardi et al. (2008) showed that the CBT can be transferred into a larger room. In the so-called Walking Corsi Task (WalCT), nine target fields are positioned on the floor in the same pattern as in the original test. Instead of using a finger to point at the target fields, the participant and the experimenter step into the fields. Piccardi et al. (2014) showed that the memory performance of children was better in the traditional CBT compared to the WalCT, while the performance of young adults was better in the WalCT compared to the CBT (Piccardi et al., 2008). The authors argued that the CBT tests peripersonal memory (in reaching space), whereas the WalCT measures extrapersonal memory (topographical space). They concluded that extrapersonal span and peripersonal span may change from child- to adulthood. However, differences in inter-stimulus intervals (ISIs) between the CBT and the WalCT may also have caused this result. In the WalCT, the experimenter and the participants take more time to walk to the fields compared to the CBT, where they only have to point at the blocks. In children, this prolonged time between stimulus presentation and recall can lead to performance degradation, as young children lack the ability to use mnemonic strategies (e.g., rehearsal), while young adults may profit from the extra time by using efficient mnemonic strategies (Ornstein, 1978). We therefore argue that it is important to use the same ISIs in embodied and control conditions to reveal potential advantages of embodiment.

In a within-subjects design, the current study tested four different conditions where encoding and recall were carried out while either standing or walking (embodied). Embodiment effects have been shown for cognitive domains like episodic memory (Dijkstra et al., 2007), science learning (Kontra et al., 2015; Lindgren et al., 2016), learning number magnitude representations (Link et al., 2013), mental imagery and rotation (Frick et al., 2009; Krüger et al., 2014), and spatial memory (Rieser et al., 1994; So et al., 2014, 2015; Schaefer, 2019). We therefore predicted that embodied conditions would lead to better memory performance than non-embodied conditions (encoding or recall while walking > encoding or recall while standing). Concerning age-specific outcomes, we expected children to profit more from embodiment than young adults, as indicated by theoretical assumptions (Piaget, 1975; Pouw et al., 2014) and experimental studies (Rieser et al., 1994; Link et al., 2013; Hainselin et al., 2017; Schaefer, 2019). On the other hand, we expected older adults to be impaired by the walking conditions due to their increased need to compensate for sensory and motor declines by investing attentional resources into motor tasks (Woollacott and Shumway-Cook, 2002; Schaefer, 2014), and because older adults may be less embodied than younger participants (Costello and Bloesch, 2017).

Furthermore, it seemed possible that the effect of context-dependent memory would influence memory performance (see meta-analysis by Smith and Vela, 2001). In a classical study, Godden and Baddeley (1975) tested divers in a free recall task. Participants learnt and recalled lists of words either on land or underwater. The results showed that more words could be recalled when learning and retrieval had taken place in the same environment. McClelland and Rumelhart (1985) explained retrieval as a reinstatement of prior patterns of activation, meaning that sensory cues, which are a fragment of the original state, are used to reinstate the mental state experienced during prior activation (see also Dijkstra and Zwaan, 2014). In the current study, this sensory input did change with conditions (recall/encoding while standing or walking), which created context-dependent cues that could affect retrieval. Therefore, we expected better performance in congruent conditions (encoding and recall while walking, henceforth denoted as "walking-walking" and encoding and recall while standing, henceforth denoted as "standing-standing") compared to incongruent conditions (encoding while walking and recall while standing, "walking-standing" and encoding while standing and recall while walking, "standing-walking"), with the congruent embodied condition (walking-walking) leading to the best memory performance.

The predicted performance patterns were preregistered and can be found using the following links: young adults: https://aspredicted.org/blind.php?x=nm2sc5; children and older adults: https://aspredicted.org/blind.php?x=3bd6vq.

MATERIALS AND METHODS

Participants

Previous embodiment studies revealed large- to medium-sized effects (Manzi and Nigro, 2008; So et al., 2014, 2015). An *a priori* power analysis with power (1-β) set at 0.80 and $\alpha = 0.05$ indicated a required sample size of 24 participants per group to detect a medium effect with $f = 0.25$ in a repeated measures ANOVA. Due to the Corona pandemic, we only managed to test 16 children, 28 young adults, and 20 older adults. Participants were tested in our laboratory at Saarland University or in a room close to a sports club (see **Table 1** for descriptives). All young adults were university students taking part for course credit. Children and older adults were contacted through local sports clubs. All participants had normal or corrected-to-normal vision and hearing and signed informed consent. In the case of children, the form was signed by a legal guardian. As a background variable, perceptual speed was measured with the Digit-Symbol Substitution task. Our participants' scores were comparable to those of corresponding age groups (Wechsler, 1981). The study was approved by the Ethics Committee of Saarland University.

Experimental Tasks

Spatial Memory Task

The Spatial Memory Task is a modified version of the traditional Corsi Block-Tapping Task (CBT) that measures participants' short-term memory capacity for visuo-spatial information (Corsi, 1972). To investigate the effects of embodiment on visuo-spatial memory, we created a spatial memory task that allows for full-body movement. We positioned 9 target fields (25 cm

× 25 cm) in a standard random configuration on a large square carpet (2.5 m × 2.5 m). Participants' goal in the Spatial Memory Task is to encode and recall sequences of increasing length by reproducing positions of target fields in the correct order. The target fields were illuminated by a beamer that had been mounted to the ceiling. Target stimuli were presented with an ISI of 3 s (see **Figure 1** for the experimental setup). Participants encoded the target fields either while standing on the starting field, or while walking to each illuminated field, from target to target. After the last target field of a sequence was presented, a visual signal indicated the end of the trial. The participant then reproduced the series of target fields. Depending on the condition, the series of target fields was either reproduced by pointing at the respective locations with a laser pointer in the correct order, or by walking to the respective target fields. The series lengths ranged from 2 targets to a maximum of 11 targets with 3 trials per sequence length for children and older adults. Young adults started with a sequence length of 3. In total, 4 lists of sequences were created by a computer algorithm. During recall, participants had to indicate the target field for approximately 1 s before pointing or walking to the next target field. The experimenter recorded the sequence of answers for each trial and compared it to a paper-and-pencil template with the correct solution. If a participant failed to reconstruct the sequence correctly in all trials of one difficulty level (e.g., all 3 trials of length 6), the Spatial Memory Task ended. The dependent variable for each condition was the sum of correctly reproduced sequences.[1] To make the scores of children, young adults, and older adults comparable, the memory performance of the sequences with a length of 3 were scored twice (this compensates for the trials with sequence length 2 that were not carried out in the group of young adults).

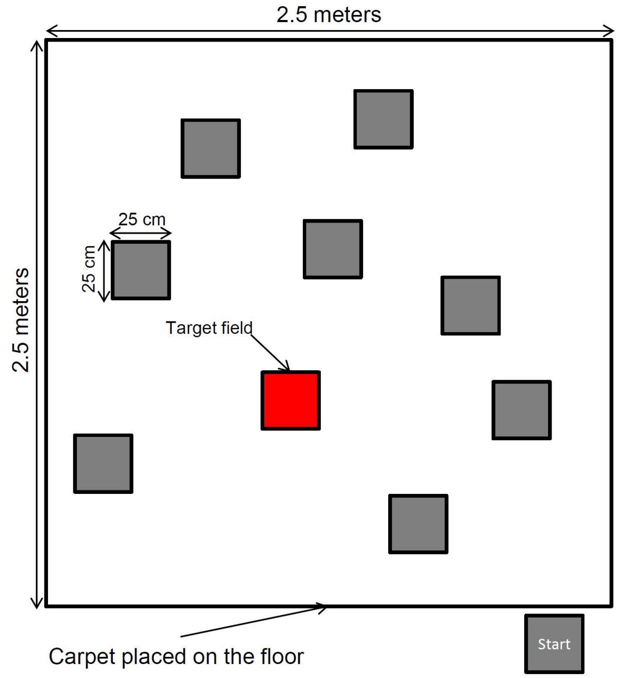

FIGURE 1 | Experimental setup of the spatial memory task, with one illuminated target field.

Procedure

Participants were tested individually in two testing sessions. Each session lasted about 1 h. The first started with the Digit-Symbol Substitution task. After that, each participant worked on the Spatial Memory Task under four different conditions: encoding and recall were carried out while either standing or while walking (standing-standing, standing-walking, walking-standing, walking-walking, see above). The order of conditions was counterbalanced with a 2 × 2 Latin Square design, while the lists of stimuli were always used in the same order for each participant (e.g., list 1 for the first trial, list 2 for the second trial, etc.). The encoding condition always stayed the same within one session. Two practice trials were carried out before starting a new condition. The ISI of 3 s was long enough to allow participants to reach the respective target field without running. For exploratory purposes, young adults also performed a tunnel task (Gramann et al., 2005, 2010), which distinguishes the navigational strategies of "Turners" and "Non-Turners," at the end of the second session. A description of the results of this task and its relation to the present study findings can be found in **Supplementary Material 1**.

TABLE 1 | Descriptives for each age group.

	Children	Young adults	Older adults
N (males/females)	16 (0/16)	28 (20/8)	20 (10/10)
Age			
Mean (SD)	10.5 (1.37)	22.11 (2.33)	72.5 (4.22)
Digit-symbol substitution task [symbols per second]			
Mean (SD)	0.41 (0.10)	1.17 (0.16)	0.44 (0.08)

Data Analysis

The Spatial Memory Task was analyzed with a mixed-design analysis of variance (ANOVA) with condition (4: walking-walking, walking-standing, standing-walking, standing-standing) as the within-subjects factor and age groups (3: children, young adults, older adults) as the between-subjects factor. A second analysis of the Spatial Memory Task was conducted with an ANCOVA to interpret the portion of variance explained by age when controlling for cognitive speed (Digit-Symbol Substitution performance). F-values and *partial Eta square* values for effect sizes are reported. The Mauchly-test of sphericity was violated for the within-subjects-factor condition of the ANOVA. Therefore, the respective results are reported using Greenhouse-Geisser corrections. The alpha level used to interpret statistical significance was $p < 0.05$. Significant main effects were further investigated by planned t-tests with Bonferroni-corrected levels of significance. For paired-samples t-tests, we present Cohen's d_z effect sizes, and for independent-samples t-tests, we present Cohen's d effect sizes.

RESULTS

The results of the ANOVA show a significant main effect of age group, $F(2, 61) = 48.224$, $p < 0.001$, $\eta^2{}_p = 0.613$. Independent t-tests with Bonferroni-corrected alpha-error probability to $p = 0.016$ indicate that the young adults' performance ($M = 13.37$, $SD = 2.31$) was better than that of the children ($M = 8.17$, $SD = 1.99$), $t(42) = 7.54$, $p < 0.001$, $d = 2.36$, and that of the older adults ($M = 8.83$, $SD = 1.30$), $t(43.95) = 8.67$, $p < 0.001$, $d = 2.54$, while children's performance was comparable to that of the older adults, $t(34) = 1.19$ $p = 0.242$, $d = 0.40$. **Figure 2** depicts the pattern of findings for each age group.

Furthermore, the main effect of condition was significant, $F(2.70, 164.56) = 117.993$, $p < 0.001$, $\eta^2{}_p = 0.659$. Paired t-tests with the Bonferroni-corrected level of significance to $p = 0.008$ indicated that memory performance was best when participants were standing during encoding and recall (standing-standing condition: $M = 14.56$, $SD = 4.03$), followed by performance in the standing-walking condition ($M = 11.66$, $SD = 4.08$), both of which were significantly better than the walking-walking condition ($M = 8.22$, $SD = 3.33$) and the walking-standing condition ($M = 8.16$, $SD = 3.14$). The difference between the latter two conditions did not reach significance (see **Table 2** for follow-up analysis). In addition, there was a significant interaction of condition and age group, $F(5.40, 164.561) = 5.732$, $p < 0.001$, $\eta^2{}_p = 0.158$. Paired-samples t-tests with Bonferroni-corrected levels of significance to $p < 0.008$ showed that the pattern of findings is identical to the main effect of condition for children and young adults, but older adults were impaired more strongly by walking during recall. Only older adults showed additional performance decrements in the walking-walking condition compared to the walking-standing condition (see **Table 2** for comparisons, **Figure 2** for the pattern of findings, and **Figure 3** for individual performances by condition).

To investigate how the observed findings are influenced by age group differences in cognition, we ran an ANCOVA controlling for Digit-Symbol scores. The ANCOVA did not reveal a significant main effect of age group, $F(2, 60) = 0.262$, $p = 0.770$, $\eta^2{}_p = 0.009$, but a significant main effect of the Digit-Symbol score, $F(1, 60) = 12.149$, $p < 001$, $\eta^2{}_p = 0.168$, showing that a substantial portion of variance of age group is explained by differences in cognitive speed. However, the interaction of condition and age group continues to reach significance, $F(6, 180) = 2.841$, $p = 0.011$, $\eta^2{}_p = 0.087$, indicating that age group has an effect on performance in the different conditions after controlling for cognitive speed. The interaction of condition and Digit-Symbol score did not reach significance, $F(3, 180) = 1.218$, $p = 0.304$, $\eta^2{}_p = 0.020$.

DISCUSSION

The current study aimed to provide evidence for the positive effects of embodiment on spatial memory using an extended version of the traditional CBT. The results showed that embodiment (walking during encoding or recall) did not enhance memory performance, but reduced memory performance significantly, especially if participants walked while encoding. Furthermore, we did not find a consistent positive effect of congruent conditions compared to incongruent conditions. Although participants reached the highest scores in the standing-standing condition, their performance levels in the walking-walking condition were very low. This indicates that this result was caused by the negative effect of walking as such rather than by the congruency effect.

Pouw et al. (2014) explained two mechanisms at work behind the embodied cognition framework. The first is "embodiment," meaning that cognitive processes can draw on previous sensorimotor experiences. The second is "embeddedness," which states that perceptual and interactive richness may assist in alleviating cognitive load. The current study showed that neither "embodiment" (e.g., conditions where recall took place after encoding with concurrent walking) nor "embeddedness" (e.g., conditions where encoding or recall took place with concurrent walking) enhanced cognition.

Contrary to our predictions, walking to the target fields during encoding and recall led to performance decrements. What mechanisms can explain this finding? Our hypothesis was grounded on the concept of embodied cognition, which states that multi-sensory information, including motor information, can improve memory performance (Barsalou, 1999; Wilson, 2002). In this context, previously experienced sensory information can work as a cue during retrieval, by aiding reinstatement of the same mental state as during encoding (McClelland and Rumelhart, 1985; Dijkstra and Zwaan, 2014). In addition, enhanced memory encoding can be expected when information is perceived by more than one modality during encoding (Bahrick and Lickliter, 2014). However, it is possible that the perception of one's own motor information interfered with the encoding and recall of the spatial positions. Moving and navigating to the target fields requires constant updates of one's own position and the positions of the target fields, which possibly created a cognitive-motor dual-task (Kahneman, 1973, 2011; Navon and Gopher, 1979; Schaefer, 2014). Walking while working on an episodic memory task has often been shown to reduce memory performance (Lindenberger et al., 2000; Li et al., 2001; Krampe et al., 2011). In the current study we found that memory performance was particularly disturbed when participants moved during encoding. We assume that encoding the sequence of target fields required more attentional resources than recalling them, leading to more pronounced performance reductions for encoding-while-walking conditions (Wickens, 1980, 1991). Furthermore, the perceived motor information while encoding could have been too undifferentiated to provide helpful cues for the reconstruction of the order of target fields. Instead, it may have interfered with the encoding of other more relevant information (e.g., visual patterns of the fields).

It is possible that our choice of ISIs of 3 s increased task difficulty in the encoding-while-walking conditions. Although participants were always able to reach each target field in time, detecting the next target field, and then walking to it probably required attention, and did not leave room for the use of elaborate encoding strategies. Using identical ISIs for both encoding conditions is an important feature of our experimental paradigm,

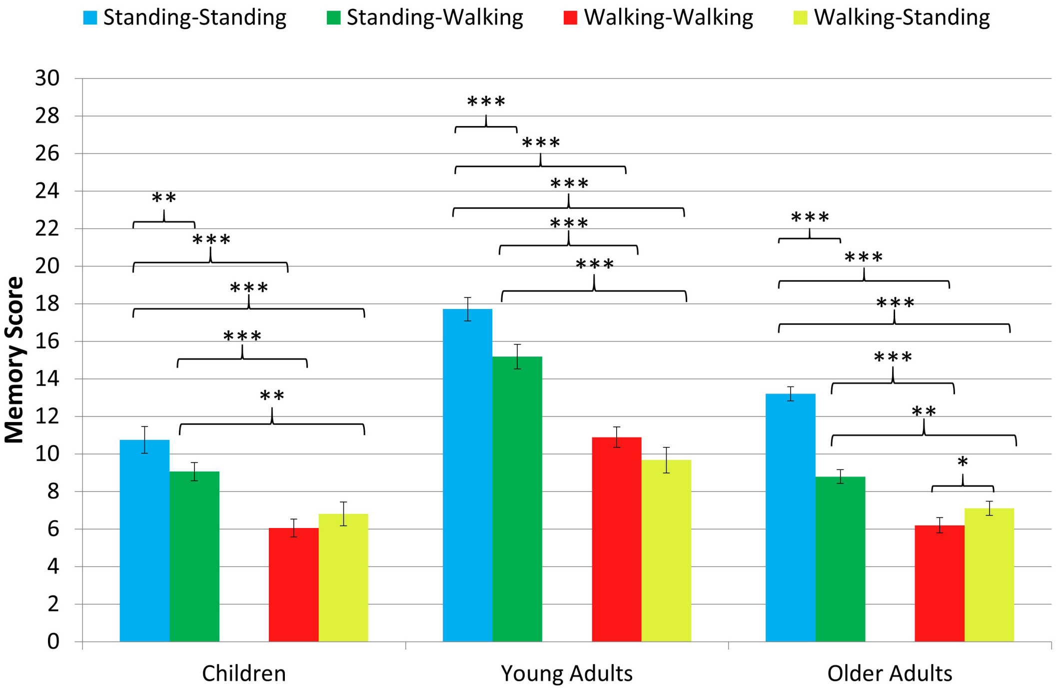

FIGURE 2 | Memory score in the spatial memory task for the four combinations of encoding and recall conditions in each age group. Asterisks indicate the level of significance ($p < 0.001$***, $p < 0.01$**, $p < 0.05$*). Non-significant comparisons are not depicted. Error bars = standard error means.

TABLE 2 | Follow-up analysis for main effect of condition and the interaction of condition and age group.

	Paired *t*-tests for the main effect condition		Paired *t*-tests for the interaction of condition × age group	
Pairs	**Overall**	**Children**	**Young adults**	**Older adults**
Walk-walk vs. Walk-stand	$t(63) = 0.16$, $p = 0.873$, $d_z = 0.02$	$t(15) = 1.49$, $p = 0.158$, $d_z = 0.37$	$t(27) = 1.61$, $p = 0.11$, $d_z = 0.30$	$t(19) = 2.39$, $p = 0.027$, $d_z = 0.53$
Walk-walk vs. Stand-walk	$t(63) = 9.03$, $p < 0.001$, $d_z = 1.13$	$t(15) = 6.57$, $p < 0.001$, $d_z = 1.64$	$t(27) = 5.66$, $p < 0.001$, $d_z = 1.07$	$t(19) = 6.40$, $p < 0.001$, $d_z = 1.43$
Walk-walk vs. Stand-stand	$t(63) = 15.07$, $p < 0.001$, $d_z = 1.88$	$t(15) = 8.84$, $p < 0.001$, $d_z = 2.21$	$t(27) = 8.42$, $p < 0.001$, $d_z = 1.60$	$t(19) = 14.23$, $p < 0.001$, $d_z = 3.18$
Walk-stand vs. Stand-walk	$t(63) = 8.74$, $p < 0.001$, $d_z = 1.09$	$t(15) = 4.32$, $p < 0.008$, $d_z = 1.08$	$t(27) = 8.60$, $p < 0.001$, $d_z = 1.63$	$t(19) = 3.96$, $p < 0.008$, $d_z = 0.89$
Walk-stand vs. Stand-stand	$t(63) = 13.88$, $p < 0.001$, $d_z = 1.74$	$t(15) = 7.24$, $p < 0.001$, $d_z = 1.81$	$t(27) = 9.48$, $p < 0.001$, $d_z = 1.79$	$t(19) = 14.03$, $p < 0.001$, $d_z = 3.14$
Stand-walk vs. Stand-stand	$t(63) = 8.78$, $p < 0.001$, $d_z = 1.10$	$t(15) = 3.18$, $p < 0.008$, $d_z = 0.80$	$t(27) = 4.24$, $p < 0.001$, $d_z = 0.80$	$t(19) = 15.46$, $p < 0.001$, $d_z = 3.46$

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[1] *An alternative analysis of the results using memory span as the dependent variable for memory performance can be found in* ***Supplementary Material 2.***

because allowing for more encoding time in embodied conditions (Piccardi et al., 2008) would not represent fair comparison. Using considerably longer ISIs would enable participants to use more elaborate encoding strategies, for example by creating a spatial representation of the path between individual fields, or by inventing a numeric system to encode individual fields and their order. We assume that increasing the ISIs of task would increase its reliance on episodic memory. Future research should investigate whether permitting longer encoding times between individual stimuli would influence the pattern of results.

Regarding the different age groups, we found comparable performances for children and older adults in the Spatial Memory Task, with young adults showing superior performances. As discussed before, there was no positive effect of embodiment in any of the age groups. In addition, the pattern of results did not differ between children and young adults, forcing us to dismiss our initial hypothesis that children may profit more from embodiment than adults. Although embodiment may help in cognitive tasks that involve learning or understanding (Link et al., 2013; Kontra et al., 2015; Lindgren et al., 2016)

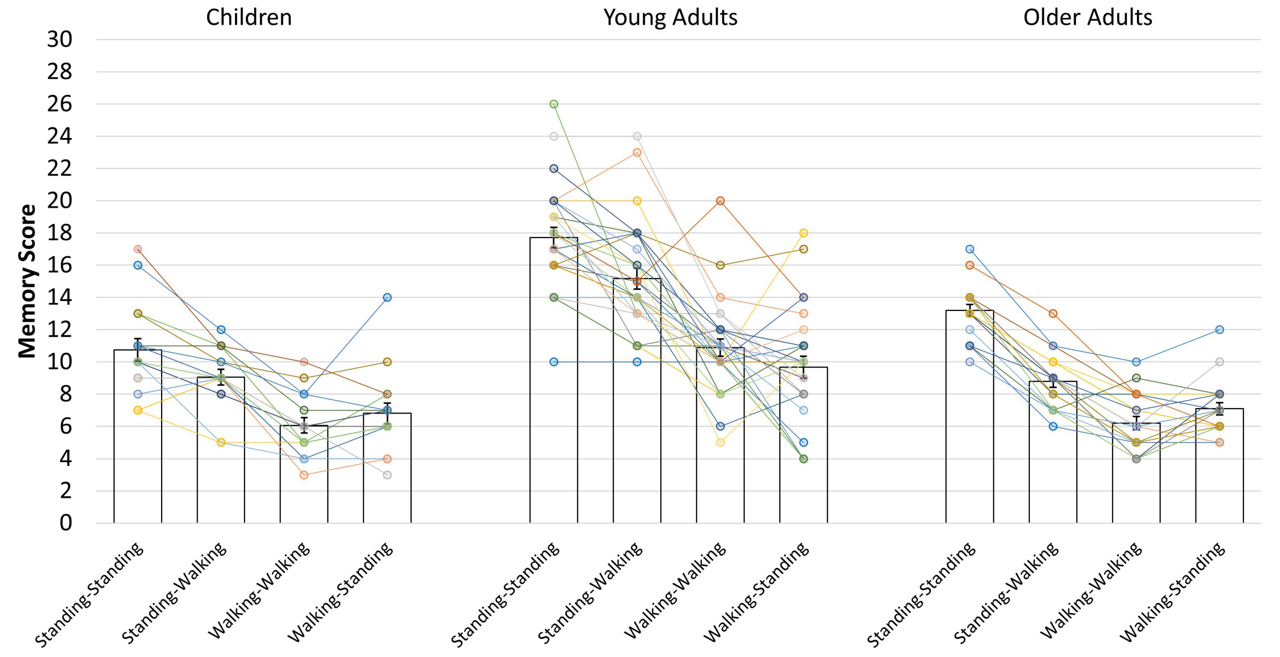

FIGURE 3 | Individual data points of the spatial memory task for the four combinations of encoding and recall conditions in each age group. Bars indicate mean scores with standard error means. Data points connected by lines indicate the performances of single participants in each age group.

and episodic memory (Dijkstra et al., 2007; So et al., 2015), embodiment may be of limited use for enhancing spatial working memory. A recent study by Amico and Schaefer (2021) also failed to find performance enhancements due to embodiment when children, adolescents and young adults were asked to encode number sequences. Embodiment was implemented there by asking participants to move to specific positions in space during encoding. The spatial locations corresponded to the to-be-encoded number. Contrary to predictions, recall performances were decreased when the encoding phase consisted of running to the corresponding gymnastic mat in a gym hall, as compared to a sitting encoding condition, except for the youngest age group (8-year-olds). However, a study by Schaefer (2019) showed positive effects of embodiment in a spatial version of the n-back task in children aged 7 years, but not in 9-year-olds. In the current study, children were about 10 years old, which leaves the possibility that younger children could have profited from embodiment. This assumption can be supported by the developmental interrelatedness of spatial navigation and self-locomotion (Anderson et al., 2013) and by theories of cognitive development that assume that physical experiences are substantial at the very early stages of life and become less important with increasing age (Piaget, 1975). If learners do indeed disembed their mental activity from the environment over time (Pouw et al., 2014), a crucial challenge for future studies is to target suitable age groups to reveal these effects.

We expected older adult's memory performance to be impaired by the walking conditions due to age-related deteriorations in sensory and motor performances (Woollacott and Shumway-Cook, 2002; Schaefer, 2014). This hypothesis was also supported by the assumption of Costello and Bloesch (2017), who describe older adults as less embodied, because they rely more on visual than on sensorimotor information compared to young adults. In the current study, memory performance was impaired, not only in older adults but also in children and young adults, if they walked during encoding or recall. However, older adults' performances deteriorated even more strongly compared to the other age groups. We assume that older adults' limited cognitive resources and their higher need to invest cognitive resources into the motor domain caused these differences. Unlike children and young adults, older adults were less able to compensate for the additional cognitive load of walking during recall. Since gender was not distributed equally across the age groups, we were not able to investigate gender as an additional between-subjects factor. This should be done in further experiments. In addition, future research with larger sample sizes per group should also assess the influence of underlying motor and cognitive skills in each age groups, since the performances in embodied cognition tasks are not only influenced by age *per se*. This is also reflected in the rather large proportion of variance in navigation performance that was explained by the cognitive speed measure (Digit-Symbol score) in the current study.

Finally, we expected equal encoding and recall conditions (standing-standing, walking-walking) to show higher memory performance compared to unequal conditions (standing-walking, walking-standing). In previous studies, information was recalled better if the conditions during recall and encoding stayed the same (e.g., occurring in the same environment, see Godden and Baddeley, 1975; Smith and Vela, 2001). The results of the current study cannot fully support this hypothesis. As shown by the main effect of condition, standing during encoding and recall elicited the highest scores, while walking during encoding and recall resulted in very poor performances. We argue that the negative effects of walking caused these effects, and not congruency. Future studies investigating the effect of context-dependent memory should manipulate the environment or the mental or bodily state of the participants.

It is an open question how embodiment would have affected spatial working memory performance if we had only asked for gestures rather than full-body movements, for example by using the setup of the traditional CBT. Would pointing to or touching the targets during encoding and recall create enough sensory input to be helpful in distinguishing the positions of the targets? A study by Chum et al. (2007) supports this idea. They showed that young adults were better at encoding and retrieving the positions of sequences of circles or squares when they used their finger to point at the targets, compared to their performance when they only watched and verbally encoded the positions. Eliminating full-body movements would also reduce the problem of altered points of view of the respective participant between embodied and non-embodied conditions. These may have increased cognitive load and had consequences for egocentric or allocentric strategies applied in spatial tasks (Chum et al., 2007). In the present context, this could be further elaborated by including a standing condition where participants watch the stimuli while standing in the middle of the carpet rather than standing at the corner of the carpet. It is also possible that the use of full-body movements to encode locations does not occur frequently in our daily life, and thus our participants were not familiar with this strategy. Future studies should familiarize and train participants in the encoding-while-walking condition to investigate whether the negative effects of walking are a result of insufficient training, or whether walking as a memorization strategy generally requires more resources than pointing or watching do. If the latter held, a differentiation between embodiment with and without full-body movements is required, especially with regard to spatial memory.

CONCLUSION

In conclusion, further research should determine the mechanisms that underlie the effects of embodied cognition, as it is strongly affected by age, cognitive resources, the kind of movement used, and the type of cognitive task applied. To date, there is a lack of age-comparative studies, and studies investigating embodiment in the domain of spatial working memory. Our findings indicate that embodiment has its limits in improving cognitive performance, and may sometimes even lead to performance deterioration caused by the need for additional body movements.

DATA AVAILABILITY STATEMENT

The raw data that support the conclusions of this article will be made available by the authors upon request without undue reservation.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by the Ethics committee of Saarland University. Written informed consent to participate in this study was provided by the participants' legal guardian/next of kin.

AUTHOR CONTRIBUTIONS

GA analyzed and interpreted the data, with input from SS. GA led the drafting of the manuscript, with contributions from SS. Both authors contributed to the study design and cooperated in conducting the literature review.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpsyg.2021.688174/full#supplementary-material

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Shared Representations in Athletes: Segmenting Action Sequences From Taekwondo Reveals Implicit Agreement

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How do athletes represent actions from their sport? How are these representations structured and which knowledge is shared among experts in the same discipline? To address these questions, the event segmentation task was used. Experts in Taekwondo and novices indicated how they would subjectively split videos of Taekwondo form sequences into meaningful units. In previous research, this procedure was shown to unveil the structure of internal action representations and to be affected by sensorimotor knowledge. Without specific instructions on the grain size of segmentation, experts tended to integrate over longer episodes which resulted in a lower number of single units. Moreover, in accordance with studies in figure-skating and basketball, we expected higher agreement among experts on where to place segmentation marks, i.e., boundaries. In line with this hypothesis, significantly more overlap of boundaries was found within the expert group as compared to the control group. This was observed even though the interindividual differences in the selected grain size were huge and expertise had no systematic influence here. The absence of obvious goals or objects to structure Taekwondo forms underlines the importance of shared expert knowledge. Further, experts might have benefited from sensorimotor skills which allowed to simulate the observed actions more precisely. Both aspects may explain stronger agreement among experts even in unfamiliar Taekwondo forms. These interpretations are descriptively supported by the participants' statements about features which guided segmentation and by an overlap of the group's agreed boundaries with those of an experienced referee. The study shows that action segmentation can be used to provide insights into structure and content of action representations specific to experts. The mechanisms underlying shared knowledge among Taekwondoists and among experts in general are discussed on the background of current theoretic frameworks.

Keywords: action perception, shared representations, athlete, expert, Taekwondo, action segmentation, embodied cognition, action understanding

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INTRODUCTION

Athletic performance is built on and might even extend the embodied representation of action (Beilock et al., 2008; Debarnot et al., 2014). Expert athletes specialized in specific actions form multimodal representations which are modified during years of training. The multimodal character of action representations becomes apparent, for instance, when motor knowledge is recruited in purely perceptual tasks (Aglioti et al., 2008) or when action and perception interfere (Alaerts et al., 2009; Zwickel and Prinz, 2012). Mostly for the visual domain, it has been frequently shown that athletes excel at tasks that require discriminating and predicting the actions from their own sport (Abernethy and Zawi, 2007; Smith, 2016). This is not only due to visual familiarity that results from countless times observing others during their sport but is supported by experience with the motor programs in addition (Aglioti et al., 2008; Mulligan et al., 2016). Expert athletes activated the sensorimotor system of the brain more while observing and predicting actions that they were able to perform themselves (Calvo-Merino et al., 2006; Balser et al., 2014; Apšvalka et al., 2018). Correspondingly, predicting and discriminating action can be improved by mere motor training (Casile and Giese, 2006; Aglioti et al., 2008). The interaction between perception and action might be tightened by plastic changes in the sensorimotor system which correlate with motor skill achievement (Hänggi et al., 2010; Wenger et al., 2017).

Plastic changes as a result of expertise in sport shape action representations, leading to shared knowledge among individual athletes (Schack and Mechsner, 2006; Abernethy and Zawi, 2007; Bläsing, 2014; Frank et al., 2015). Besides benefits during physical performance, shared knowledge can facilitate the perception and anticipation of action and the communication about the specific domain of expertise (Abernethy et al., 2005; Aglioti et al., 2008; Mann et al., 2010; Güldenpenning et al., 2011; Kunde et al., 2011). The topic of shared representations in sport has been addressed frequently in the context of team interaction (Rentsch and Davenport, 2006), where it was shown that teams represent not only their own but also team members' intentions. The activation of sensorimotor functions during action perception is a potential mechanism that could underlie the understanding of teammates (Blakemore and Decety, 2001). When individuals who are on a similar level of expertise observe each other, a better match between the sensorimotor knowledge and perceived action can be assumed (Calvo-Merino et al., 2006; Schubotz, 2007; Diersch et al., 2013). However, not only sensorimotor knowledge plays a role in action understanding and interaction in sport but also semantic representations as well as strategic and normative knowledge (Rentsch and Davenport, 2006; Debarnot et al., 2014; Vesper et al., 2016). Another aspect is the level of interaction which is required to build shared representations. Besides studies in interacting teams, there are results indicating that shared representations might also exist between people who frequently engage in the same activities without interacting. For instance, it was shown that climbers had individually established the same action categories in relation to different grip shapes (Bläsing et al., 2014).

Extending this research, we studied whether indicators for shared representations can also be found in intransitive actions, i.e., when actions are not determined by the characteristics of external objects such as grips or tools. Moreover, it is an open question whether elaborate action representations would apply to unfamiliar actions from the athletes' respective discipline. In order to measure shared representations, we used the so called "event segmentation task" (Newtson, 1973; Zacks et al., 2001; Schubotz et al., 2012) and asked Taekwondo experts to parse complex movement sequences from their sport. This task is frequently employed in the context of the "event segmentation theory" (EST) (Zacks et al., 2007) which proposes that we intuitively segment the ongoing flow of information into meaningful units or "events" in order to understand and encode them. The subjective placement and grain size of segmentation depends on top-down influence from action representations and on bottom-up sensory cues such as observed movement kinematics and top-down influence from memory (Zacks et al., 2009). Boundaries between segments are characterized by either a decrease in perceptual coherence and/or an increase in the amount of information. Several continuations are possible at boundaries which results in a transient reduction of the predictability of the forthcoming sequence (Zacks et al., 2007; Schubotz et al., 2012; Schiffer et al., 2015). For instance, in goal directed actions, individuals largely agree on placing boundaries at action goals, reflecting that sequences are less predictable after a goal has been achieved (Levine et al., 2017).

The segmentation task is suited to study the specific influence of expertise on action representations as the sensorimotor repertoire seems to determine the parsing of observed action. In patients it was shown that segmentation performance predicted impairments in activities of daily living (Bailey et al., 2013). Moreover, reduced temporal precision during segmentation was observed in participants with Parkinson's disease (Schiffer et al., 2015). This was taken to reflect problems with movement timing known to result from dysfunctions in areas affected by the disease. That the same representations underlie segmentation and production of action is further supported by brain imaging studies. The angular gyrus in the parietal lobe and the superior frontal sulcus both associated with action selection during planning, were particularly active at boundaries between two segments (Schubotz et al., 2012). Moreover, the additional engagement of the motion sensitive temporal area (MT) suggests the attention to kinematic features at boundaries (Schubotz et al., 2012).

Beside the impact of sensorimotor impairment, also motor skill increase is reflected in action segmentation, as addressed by a few studies. Most of them involved closed-loop, mostly internally guided actions, i.e., dancing and figure skating (Bläsing, 2014; Levine et al., 2017; Di Nota et al., 2020) and recently basketball (Newberry and Bailey, 2019; Newberry et al., 2021). Different aspects were highlighted in these studies and some criteria were identified to possibly determine segmentation judgments. First, the grain size of segmentation was larger in expert dancers (Bläsing, 2014; Di Nota et al., 2020) or in amateurs after having trained the observed choreography (Bläsing, 2014). This means that amateurs marked more boundaries before they had experienced performing a dance sequence and integrated single segments into longer units after gaining motor familiarity. This effect of expertise was shown to interact with factors such as time on task (Di Nota et al., 2020) and could be changed by the explicit instruction to do fine grained segmentation (Newberry et al., 2021). A second aspect is transfer of segmentation patterns to unfamiliar actions. One study (Di Nota et al., 2020) addressed this question but found no evidence. Thus, transfer has been studied so far in one single example with Bharatanatyam dancers, an Indian dance, segmenting a ballet piece. More evidence is required here. A third aspect is inter-individual agreement about where to place boundaries in an action sequence. In videos of figure skating routines and basketball games, experts agreed on more boundaries than novices, which could indicate the use of expert knowledge (Levine et al., 2017; Newberry et al., 2021). However, in figure skating, experts and novices tended to place most boundaries at the goals of the actions or at the beginnings (Levine et al., 2017). As the authors point out, the contribution of action semantics, movement kinematics, and expert knowledge could not be clearly separated (Levine et al., 2017). Regarding basketball, the placement of boundaries could not be related to a single individual's ongoing actions but rather to interactions within teams or with opponents.

The present study aimed at dissociating the influence of shared expert knowledge from more general aspects of action semantics and movement kinematics. Moreover, it asked whether expert knowledge generalizes such that it can be applied to unfamiliar sequences from the same domain of expertise. The Taekwondo form discipline was chosen as this sport fulfills several criteria which are crucial to address these aims. In Taekwondo, athletes can specialize in movement techniques, so called "forms" or "patterns" which are continuous sequences of complex movements derived from combat actions. They are performed individually by a single athlete. Comparable to dance, forms contain intransitive actions, which are not directed toward a goal in the environment. This allowed studying shared representations without involving any external objects which could determine action types or indicate goal achievement. In order to study knowledge transfer, experts and actions from two different Taekwondo federations, World Taekwondo (WT) and International Taekwondo Federation (ITF), were involved which allowed comparing familiar to unfamiliar actions as athletes are trained according to the techniques of one particular federation. WT has 17 and ITF has 20 different forms with increasing complexity. For instance, the first forms trained by beginners are characterized by easier transitions between movements and patterns are repeated symmetrically to four sides. Higher-level forms are mastered by experts and are more complex with less repetitions. Here we chose 12 examples, 6 from each style with different complexity. In order to assess unbiased and spontaneous agreement among athletes and to point to the preferred source of information, i.e., visuomotor or semantic, no particular grain size was instructed and the participants were encouraged to set segmentation marks subjectively in the ongoing video. This is in contrast to most earlier segmentation studies which have presented single examples of a longer action sequence several times, often under different instructions, e.g., to perform fine grained after coarse grained segmentation.

We expected that under these conditions experts spontaneously integrate over longer episodes resulting in a larger grain size, i.e., lower response frequency compared to an unexperienced control group. We further hypothesized that in contrast to the control group, Taekwondoists rely on shared expert knowledge even when observing and segmenting examples of actions from the different style for the first time. High agreement within a group leads to an accumulation of responses in particular time windows which can be described as peaks in agreed event boundaries.

MATERIALS AND METHODS

Participants

A group of 24 Taekwondo experts was compared to a group of 29 novices. Four experts were Japanese and were tested in Japan [Department of Human Sciences (Psychology), Tokyo Metropolitan University]. **Table 1** provides a detailed overview over the sport-specific expertise of both groups. The remaining 20 athletes were tested in Germany, 5 of them, who were specialized in technical form Taekwondo, at a laboratory at the Chair of Human Movement Science, Technical University of Munich and 15 members of the German national Taekwondo team [Deutsche Taekwondo Union (DTU)], specialized in sparring, were tested at the occasion of a training camp. The experts had on average 15.3 ± 6.8 years of experience and trained 13.7 ± 7.2 h per week. Members of the control group were active in their respective sport since 14.6 ± 7.3 years with 4.0 ± 1.8 weekly training hours. Most of the athletes (19) were trained according to the rules of WT, the four Japanese athletes were trained according to the ITF and one athlete was experienced in both styles. Of the control participants, 11 were tested at the lab in Japan and 18 were tested in Germany. On average, the control group had 14.6 ± 7.3 years of experience in their respective discipline and trained 4.0 ± 1.8 h per week. The participants signed an informed consent and those who came to our laboratory received allowance for travel expenses. The procedure followed the standards of the Declaration of Helsinki and was ethically approved by the Ethics Committee of Tokyo Metropolitan University (H28-69) and the vote was transferred for testing in Germany.

Stimuli

Movement sequences of the two Taekwondo styles, WT (Poomsae) and ITF (Tul) were recorded using two highspeed cameras (JVC, frame rate 250 per s) for later movement analysis and a high-resolution camcorder (Sony HDR-CX900, 1080p, 50 per s) for stimulus production. The latter camera was placed at the center and the highspeed cameras more lateral, covering the standard movement areas of 8 m × 8 m in WT and 9 m × 9 m in ITF.

For each style, a male and a female athlete who were top ranked in international competitions of their federation were filmed while performing forms of lower and higher complexity. Six different Tul, number 5, 6, 7, 9, 12, and 13 were included

TABLE 1 | Details of participant sample.

Participants	**Experts** **Mean (SD); median; min; max**	**Controls** **Mean (SD); median; min; max**
N	24 (4 Japan; 20 Germany)	29 (11 Japan; 18 Germany)
Gender	15 m; 9 f	15 m; 14 f
Age	23.5 (7.4); 22.0; 18; 47	25.0 (5.3); 24.5; 20; 47 Age difference: *t*(48) = 0.86; *p* = 0.40
Experience	**Taekwondo**	**Other sports**
Taekwondo style	*N* = 19 WT *N* = WT + ITF *N* = 4 ITF	No experience in Taekwondo
	N = 15 members of German national team (DTU)	*N* = 17 game sports* *N* = 2 coordinative sport**
Experience (years)	15.3 (6.8); 16; 2.4; 31	14.6 (7.3); 17.5; 0.6; 23
Training per week (h)	13.7 (7.2);14.5; 3; 24	4.0 (1.8); 4; 1; 7.5
Duration training unit (min)	107.3 (21.1); 102.5; 90; 180	78.3 (24.9); 75;35;120
Units per week (average in last 12 months)	7.7 (4.0); 9; 2; 14	3.2 (1.4); 3; 1; 6
Participation in competitions	Currently participating = 21 No participation = 3	Currently participating = 6 No participation = 19 In the past = 4
Experience performing Taekwondo forms	No = 9 Yes = 13 Average 2.1 (1.5) times/week min 0.25; max 5.5 No response = 2	
Experience watching Taekwondo forms	No = 7; Yes = 15 No response = 2	

**To assess how many control participants had experience with coordinative sports, we included soccer, volleyball, basketball, and tennis but also endurance sport and shooting. **Gymnastics and Yoga.*

in the experiment. The numbers 5, 7, and 13 were performed by a male athlete. The six Poomsae were, number 5, 7, 8, 9, 10, and 12 and 5, 8, and 10 were performed by a male athlete (**Figure 1**). In each style, the three lower numbers are easier forms, trained by pupils, and the three higher numbers are more complex which are mastered at high-level promotions. On average, an ITF clip lasted for 51 s and a WT clip for 71 s. Four additional forms, four Poomsae and four Tul, performed by male and female models were used in a practice run and one additional clip was shown as an example during the instruction. The videos were presented on notebooks with a screen diameter of 15.6 inches (33.5 cm × 19.4 cm) and a resolution of 1366 × 768. The participants were seated at a distance of 45 cm from the screen. Form this position, the height of the athletes vertically covered a visual angle between approximately 12.7° and 16.4° which varied slightly during the movement, depending on the athlete's position in relation to the camera. The athletes' faces were blurred to avoid that observers would recognize them or interpret gaze which might have been altered due to the proximity of cameras. The software Adobe Premiere Pro was used for video processing. For stimulus control and response recording, the software Presentation (Neurobehavioral Systems) was used.

Task and Procedure

The 12 videos were presented in a pseudorandom order in an online version of the action segmentation task. Online means that the participants were required to mark boundaries during the ongoing video. In contrast to other versions of the segmentation task, they were not allowed to scroll forward or backward or to stop the video. This version of the task was chosen as it allows to interpret the timing of the marked boundaries in relation to the actions and to other participants.

At the start of the experiment, the participants were asked to place their right hand on the computer mouse. The instruction for the segmentation task was as follows: "Your task is to cut the action sequences into single pieces according to your own estimation. To do this task, press the mouse with your index finger whenever a unit is completed. Usually, at the same moment, a new unit is about to begin. There is no right or wrong in this task and your decisions are considered completely subjective."

In the beginning of an experimental session, the participants signed an informed consent form, read the task instruction and watched a video of a Taekwondo form to show them which stimuli to expect. To assess individual reaction times (RTs), they performed a 0-back task in which they were required to respond as fast as possible to the appearance of an initially defined target picture. In total 50 images of different body parts were randomly presented with a stimulus duration of 500 ms and an inter-stimulus-interval of 100 ms. Among these stimuli, the target appeared 10 times (20%). The target was randomly selected out of 10 different images showing closeups of a model's elbow, knee, feet, hands, shoulder, etc. Only responses with latencies between 100 and 1500 ms were recorded. Accuracy was recorded

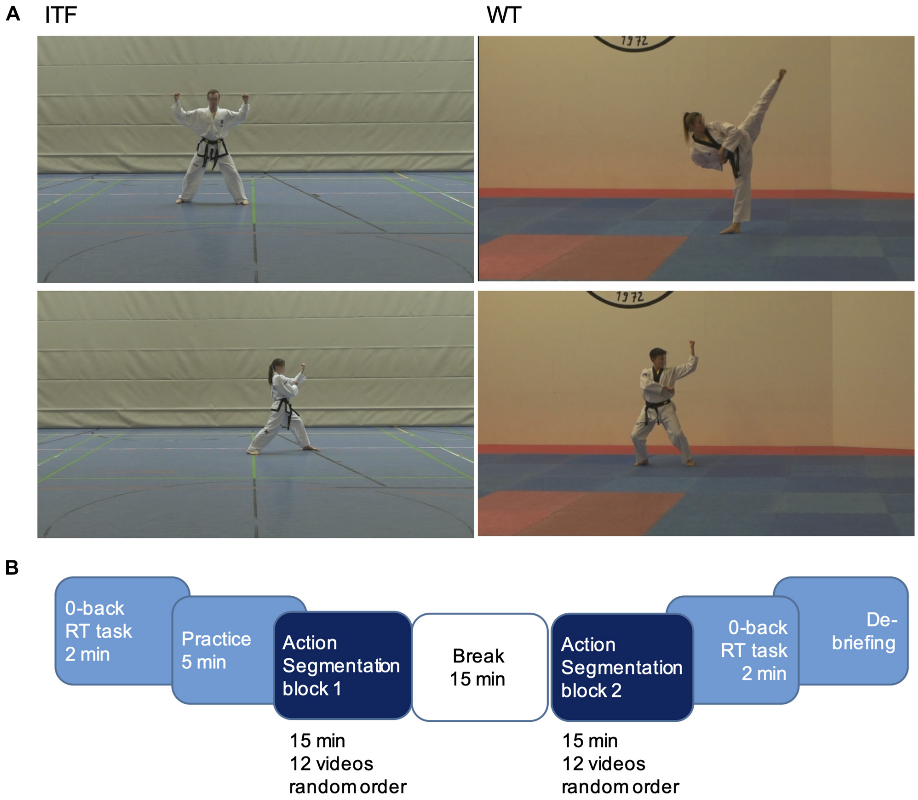

FIGURE 1 | (A) Stimuli were 12 videos showing Taekwondo form sequences performed by two athletes experienced in ITF and two in WT Taekwondo styles. **(B)** Experimental procedure.

in addition to RT. The same response mode and device was used as in the segmentation task. This was followed by a familiarization run in which the participants practiced the action segmentation task during 5 min on four clips. All participants claimed to have understood the task and proceeded to the first experimental block in which the 12 video clips were presented in pseudo-random order with no more than 3 repetitions of the same athlete or Taekwondo style. After a break of at least 15 min, a second block of the same task but with a different order of videos was performed. To test for effects of fatigue on RT, a second run of the 0-back task was performed in the end of the session using the same stimuli and procedure as in the first run in a different order. Finally, the participants filled in a questionnaire asking about their experiences in Taekwondo and in other sports and about strategies applied in the segmentation task.

Data Analysis

The average time between responses (TBR) was computed as a measure to compare the response frequency between the conditions. The parameter TBR was calculated for each participant and each clip by obtaining the duration between successive responses in seconds. It was measured from the first response onward, until the last and thus the times in the beginning and in the end of the videos in which the movement needs some time to start and no boundaries were marked, are not considered. For each participant, a measure of re-test reliability was obtained by correlating TBR averaged over all videos in block 1 with the average TBR in block 2. As a measure of within subject consistency, the rate of overlap (ROO) between responses in the two experimental blocks was determined by assessing the percentage of block 1 responses which were repeated in block 2. Responses were considered as repeated if they were overlapping within a time window which was individually defined for each participant. Its size was determined by the standard deviation (SD) of each individual's RT measured in the 0-back task. As a Wilcoxon-test did not reveal a significant difference between the two runs of the 0-back task (experts: $Z = -0.1,51$, $p = 0.13$; novices: $Z = -0.94$, $p = 0.35$), the SD was computed over all trials, separately for each subject. Thus, for each response in block 2, it was controlled whether in block 1 a response was given within a time window centered at the block 2 response ± 0.25 SD. Parameter ROO represents the percentage of responses in block 2 in which a match was found in block 1.

Measures of Between-Subject Agreement

The agreement about the placement of segmentation boundaries was assessed separately for each group and video. Thus, for each video, we counted how many participants within each group agreed on the same boundaries. The number of participants who responded within a time window of 1 s prior to each video frame ("bin") was counted. This procedure was adapted from

Schubotz et al. (2012) where it is described in more detail. Within the same bin, only one response of each participant was counted and thus the maximum possible number of responses was equal to the number of participants in the respective group. This resulted in the "added frame value" (afv) parameter. It contains the number of participants responding within each bin (**Figure 2**). In order to detect meaningful agreement, i.e., agreed boundaries (n-bound), in each video, those bins in which the afv exceeded the mean by 2 SD were identified. Means were calculated without bins with zero responses. Thus, the parameter n-bound represents above-average agreement about segmentation between participants in each group.

In the statistical analysis performed with IBM SPSS 23 we differentiated between two types of analyses.

(1) The analyses of response frequency and the response consistency were performed on values of single participants. Non-parametric tests were used since some variables were not normally distributed as tested with Shapiro–Wilk tests. Thus, for the parameters TBR and ROO, Wilcoxon tests were performed separately for experts and novices to test for differences between the styles (WT vs. ITF) and between the two experimental blocks. To test for between-group differences in TBR and ROO, Mann–Whitney *U*-tests were applied.

(2) The analyses of within group agreement on boundaries were based on the n-bound count of each single video. Thus, single videos were treated as subjects. This resulted in 12 cases, 6 ITF and 6 WT. In both styles, six videos were easy and six difficult. As each video was watched by the expert- and the control group, the group difference in n-bound was tested in a one-way repeated-measures ANOVA. Separately for each group, two multivariate ANOVAs were performed to assess the influence of (1)

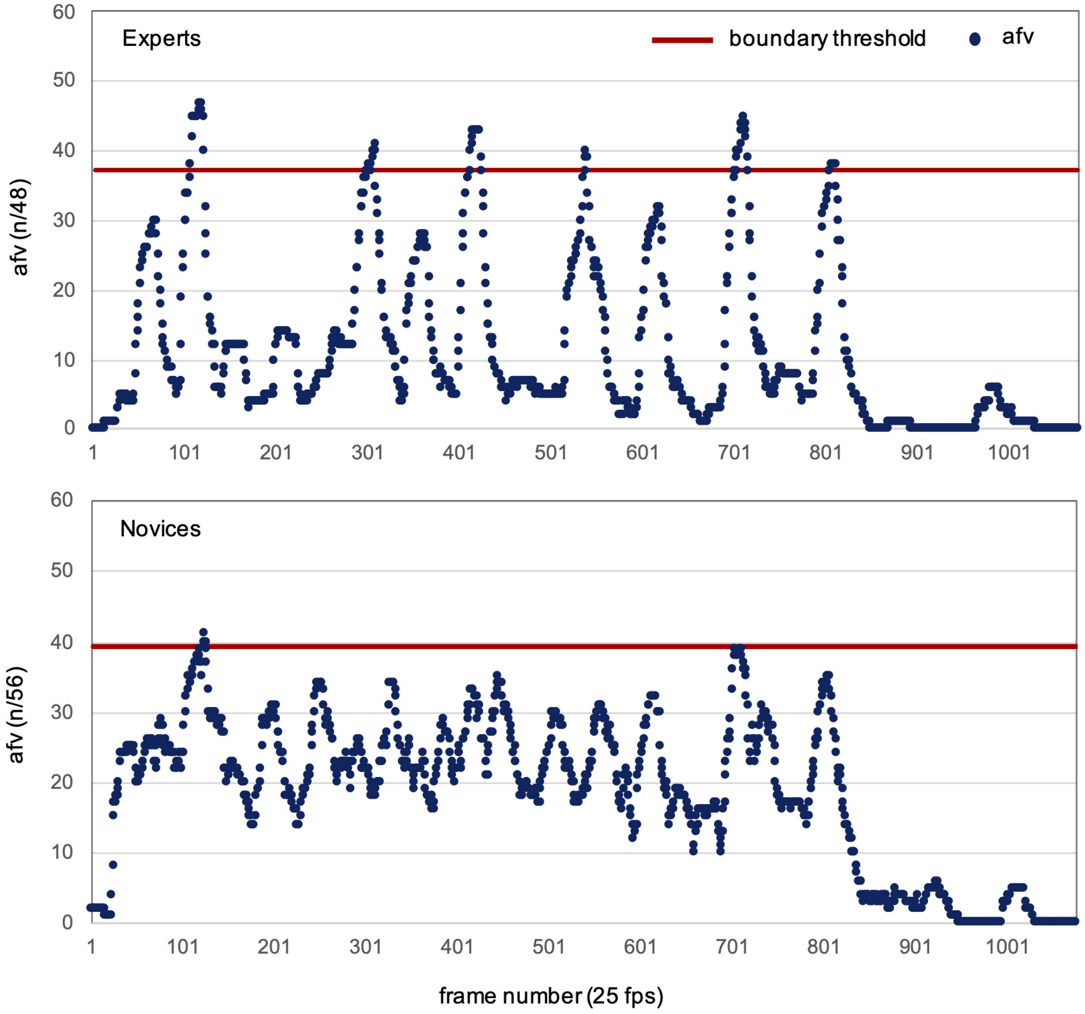

FIGURE 2 | Agreed boundaries in expert and novice groups in one exemplary video (WT Poomsae #5). The added frame values (afv, blue dots) represent the number of participants responding within each bin (i.e., within 1 s prior to each video-frame). Responses of the two blocks are summarized, thus the maximal afv achievable is double the participants in each group. Boundary threshold (red line) is 2 SD above average afv. Peaks exceeding the boundary threshold are counted (n-bound) and represent within-group agreement.

style and (2) difficulty on the outcome variables n-bound, average TBR and average ROO for each video.

Exploratory Descriptive Analyses

In addition to questions about sport specific expertise (**Table 1**), the participants were asked about strategies applied during the experiment in one multiple-choice question (**Table 2**). They could select among five different suggestions – direction change, kicks or punches, change in movement speed, predicting events in time and feeling the movement. In addition, they could indicate other criteria if applicable. In three open questions Taekwondoists were asked on experiences and thoughts during Tul/Poomsae performance and learning. Two novices and 10 athletes, all from Germany, answered the expertise questions only and did not fill in the second part due to time constraints.

The n-bound obtained within each group were compared with the boundaries defined by an expert referee who is a member of the Poomsae Referee Committee WCTU and world champion (referred to as "T4" hereafter). He was also active in training for 9 h per week. The bins in which the responses were given by T4 were graphically highlighted and superimposed on the agreed boundary graphs of the expert group (without T4) and of the control group (**Figure 5**). The overlaps were visually inspected.

Further, a video-based movement analysis was performed using the software SIMI Motion for a descriptive comparison between kinematics and boundaries. Synchronous recordings of three cameras were imported and prepared for 3D analysis. Six body parts, head, left and right hand, pelvis, left and right foot were marked in the first video frame and were tracked semi-automatically (with manual corrections) for the whole duration of the action sequence which corresponded to the duration of the same video in the segmentation experiment. From marker displacement in x, y, and z, integrated acceleration measures were obtained for all 6 markers. In order to test whether maxima in acceleration coincide with boundary marks, the acceleration profiles were treated in the same way as the afv profiles of the two groups. Thus, those periods which exceeded average acceleration by 2 SD in the positive or negative direction were marked. These profiles were graphically superimposed onto the agreed boundaries of both groups (**Figure 6**).

TABLE 2 | Debriefing questionnaire.

Criteria for segmentation	Experts %	Controls %
Direction change	56	70
Kicks or punches	39	74
Change in movement speed	56	59
Predicting events in time	67	19
Feeling the movement/simulation	56	15
Other criteria	22	37
	Attack and defense, connect meaningful events, or symmetric movement	Breaks, hand movement, and starting posture
Change of strategy	44	44

Answers to the questions "Which criteria did you use for segmentation?" and "Did you change your approach during the experiment?" In the first question, multiple selections were possible and participants could optionally indicate which other criteria they used.

RESULTS

Response Frequency and Response Consistency

No difference between the groups was found in RT in the 0-back task on images of body parts ($Z = -0.44$, $p = 0.66$). Experts needed on average 384.8 ± 59.7 ms and novices 385.71 ± 37.1 ms to respond to the presentation of the target image. Participants tested in Japan had a significantly higher mean RT (405.35 ± 43.53 ms) than those tested in Germany (377.9 ± 48.43 ms), Mann–Whitney U-test $p = 0.041$, which resulted from 10 German participants with RTs between 276 and 346 ms while for all 14 participants from Tokyo an RT of at least 357 ms or higher was recorded. In all other parameters, no significant laboratory effects were found. In the segmentation task, on average 15.1 ± 10.0 (median = 10.10) responses were given per video which can be expressed in a response rate of 0.25 ± 0.17 (median = 0.17) responses per second. A huge variation between the participants was observed, ranging from 5.1 to 35.9 responses per video.

For the statistical assessment of the effects of group, experimental block and style on the response frequency, the parameter TBR was used as outcome variable. On average, TBR was 6.64 ± 3.62 s in experts (median = 6.3; range 1.7–20 s) and 5.51 ± 3.42 s in novices (median = 5.3; range 1.7–14.1 s). Neither expertise ($Z = -1.19$, $p = 0.23$), nor style ($Z = -0.29$, $p = 0.77$) or the experimental block ($Z = -1.21$, $p = 0.23$) had a significant effect on TBR (**Figure 3A**). Also, when computed separately within the groups, no significant effects were found for block or style ($p > 0.27$).

To conclude, TBR reflected very different individual approaches but no systematic effects of group, experimental block and style. Correlations between TBR in block 1 and block 2 over the whole sample ($r = 0.86$, $p = 0.001$, $N = 52$) and within each group (experts: $r = 0.76$, $p = 0.001$, $N = 24$; novices: $r = 0.92$, $p = 0.001$, $N = 28$) pointed to a high re-test reliability regarding the individually selected grain size (**Figure 3B**). Thus, the participants kept their initial segmentation grain size.

In order to measure within subject consistency in the placement of event boundaries, the rate of overlap (ROO) was computed. No differences between groups ($Z = -1.10$, $p = 0.27$) or styles ($Z = -0.36$, $p = 0.72$) were found and the comparisons between the styles within each group were not significant ($p > 0.22$) (**Figure 3C**).

Within-Group Agreement on Boundaries

For each video, the parameter n-bound was determined which indicates how many peaks surpassed the threshold for within group agreement (**Figure 2**). To assess the effect of expertise on n-bound, the 12 videos watched by experts were compared to the same videos watched by the control group in a one-way ANOVA. As hypothesized, n-bound was significantly higher in the expert

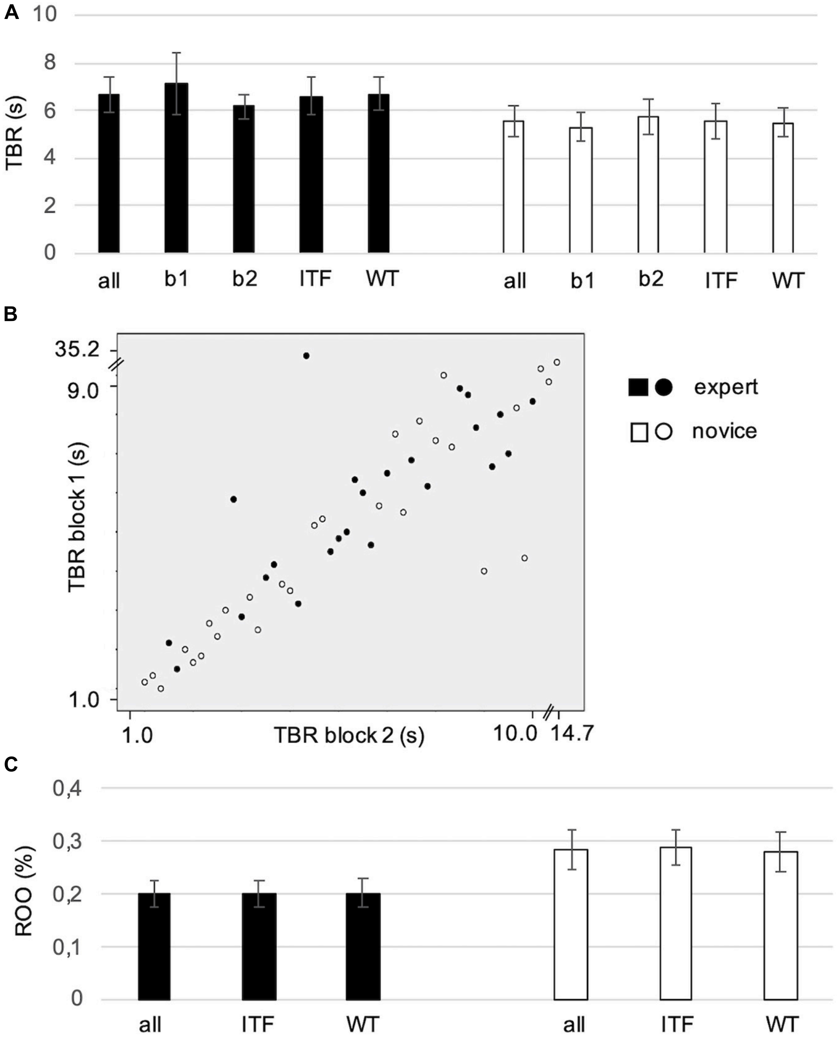

FIGURE 3 | (A) Average time between responses (TBR) in seconds (s) for experts and novices in experimental block 1 (b1) and block 2 (b2) and for two styles (ITF, WT). Error bars indicate SE. **(B)** Correlations of TBR in block 1 and block 2 for the two groups. Scales are adjusted to values and extreme values represent two outliers (expert in block 1: 35.2 s and novice in block 2: 14.7 s). **(C)** Average response overlap (ROO) expresses the rate of block 1 responses repeated in the same time window in block 2. Error bars indicate SE.

group (6.1 ± 1.31) than in the control group (3.17 ± 2.0) [$F(1,11) = 16.29, p < 0.002, \eta_p^2 = 0.6$] (**Figure 4**).

Separately for each group, two multivariate analyses of variance were performed to study the influence of either style or difficulty of the action sequence on n-bound. In order to additionally test for effects of these factors on response frequency and consistency, average TBR and ROO obtained for each video were included as additional outcome variables. In both groups, style neither had an effect on n-bound nor on TBR ($F < 0.41$, $p > 0.54$, $\eta_p^2 < 0.04$) but on ROO it had a marginal effect in the expert group [$F(1,10) < 4.10, p > 0.071, \eta_p^2 < 0.29$] and was significant in the control group [$F(1,10) = 7.38, p = 0.022, \eta_p^2 = 0.43$]. While experts tended to be particularly consistent in WT actions (WT: response overlap in 34.7 ± 12.1% vs. ITF: 24.2 ± 4.6%), novices were more consistent in ITF (ITF: response overlap in 26.2 ± 3.5% vs. WT: 21.7 ± 1.9%) (**Figure 4B**).

Difficulty did not affect n-bound and ROO in both groups [$F(1,10) < 3.5, p > 0.09, \eta_p^2 < 0.26$] but had a significant effect on TBR in experts [$F(1,10) = 6.44, p = 0.03, \eta_p^2 = 0.39$] and in novices [$F(1,10) = 8.02, p = 0.018, \eta_p^2 = 0.45$]. In both groups, TBR was shorter in easy sequences (experts: 5.26 ± 0.71 s; novices: 4.99 ± 0.62 s) than in difficult ones (experts: 6.62 ± 1.12 s; novices: 6.04 ± 0.67 s) (**Figure 4C**).

In order to address the question of transfer to unfamiliar actions, n-bound was computed for the 19 experts with WT background alone. As in the comparisons above, first, the difference to the control group was analyzed in a one-way ANOVA which resulted in a significantly higher number of n-bound in the group of WT athletes [$F(1, 11) = 61.89, p = 0.001, \eta_p^2 = 0.85$]. Comparing their agreed boundaries in the familiar WT videos to the unfamiliar ITF style revealed no difference between the two styles [$F(1, 10) = 0.26, p = 0.62, \eta_p^2 = 0.026$].

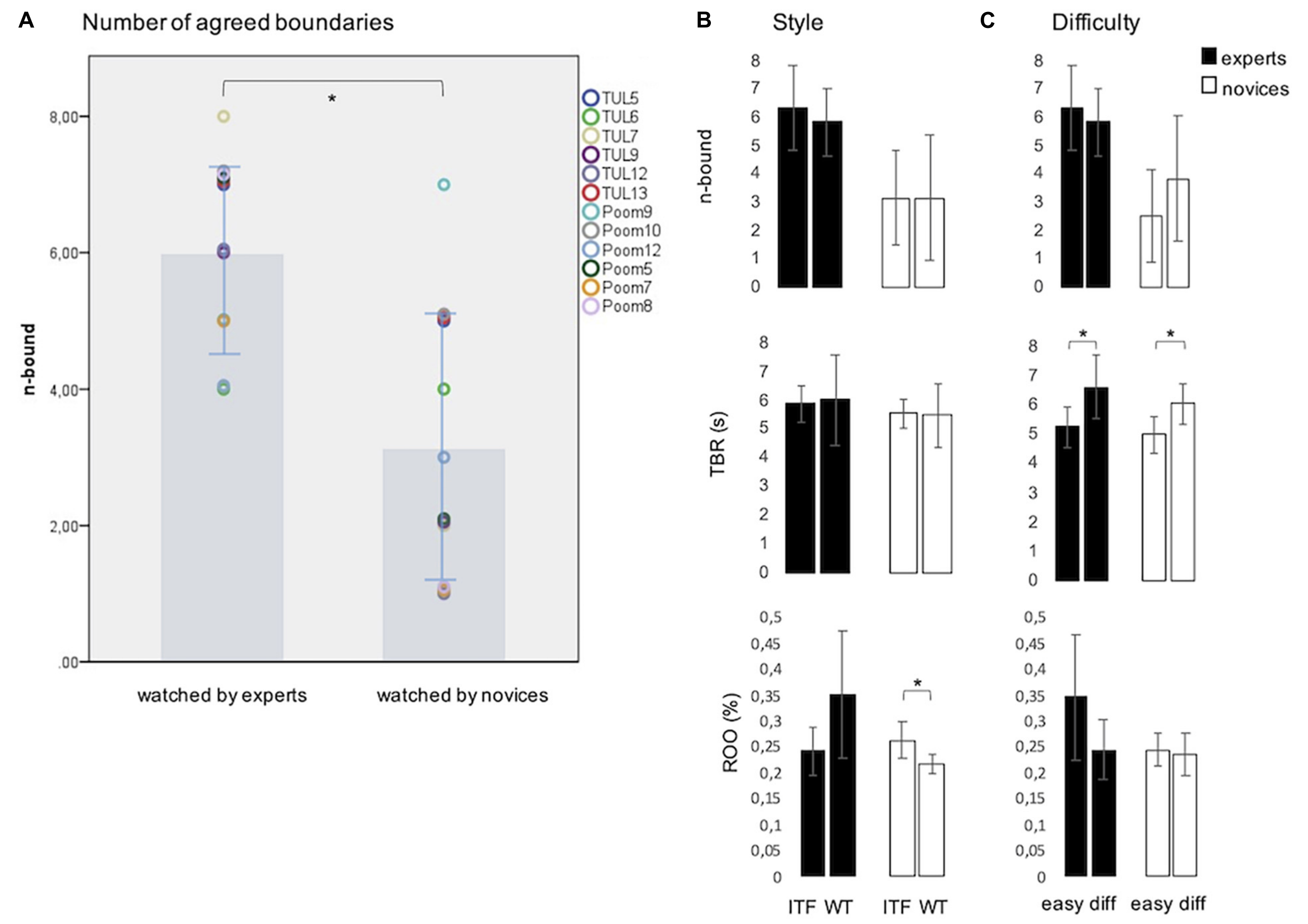

FIGURE 4 | (A) Experts agreed on a higher number of boundaries (n-bound) than novices. Colored points represent n-bound in each of the 12 single videos watched by experts and novices. **(B)** Style (ITF vs. WT) had no effect on n-bound and on average time between responses (TBR). In novices, response overlap was significantly higher in ITF than in WT actions. The high agreement in WT in experts was not significant. **(C)** The difficulty (in terms of complexity) of the action sequences only affected TBR significantly. In both groups more time passed between boundaries in difficult sequences, i.e., the grain size of segmentation increased. In all graphs, bars show mean and error bars SD. **p* < 0.05.

This indicates equal levels of agreement in familiar WT and unfamiliar ITF actions.

Exploratory Descriptive Analyses for Qualitative Inspection

Questionnaire

In additional open questions, the participants specified which other strategies they used in the task and which general observations they made. As **Table 2** shows, the control group based the segmentation more on bottom-up information. However, their open answers indicate that recurring patterns, such as the symmetric repetition of elements, were occasionally recognized by some participants. Seventeen percent of the control participants reported that they noticed that elements were repeated and that they integrated over longer sequences later in the experiment. Regarding strategy changes, the control group mostly indicated to have changed between the features listed in the questionnaire (**Table 2**). Athletes described the strategy of connecting elements more often than novices and in their reports the word "meaningful" was used several times, i.e., to have connected elements to longer meaningful segments. This could point to the employment of top-down semantic knowledge and is underlined by the use of prediction in experts. Trying to feel the movement was selected more often by experts and employs mechanisms of action simulation and imagery. Approximately half of the experts were confident with their strategy only for the familiar sequences. For the unfamiliar style, one expert reported to have "memorized the whole movement and then tried to get into the details." The same strategy was reported by one control participant.

Comparison With Judgments of Expert Referee

Comparing the responses of the referee T4 between the two blocks, it is obvious that they frequently fell into the same bins (**Figure 5**). Thus, the boundaries marked by T4 largely corresponded between the two blocks. In experts, afv-peaks overlapped more often and more precisely with the responses of T4 than the afv maxima in novices. This precise

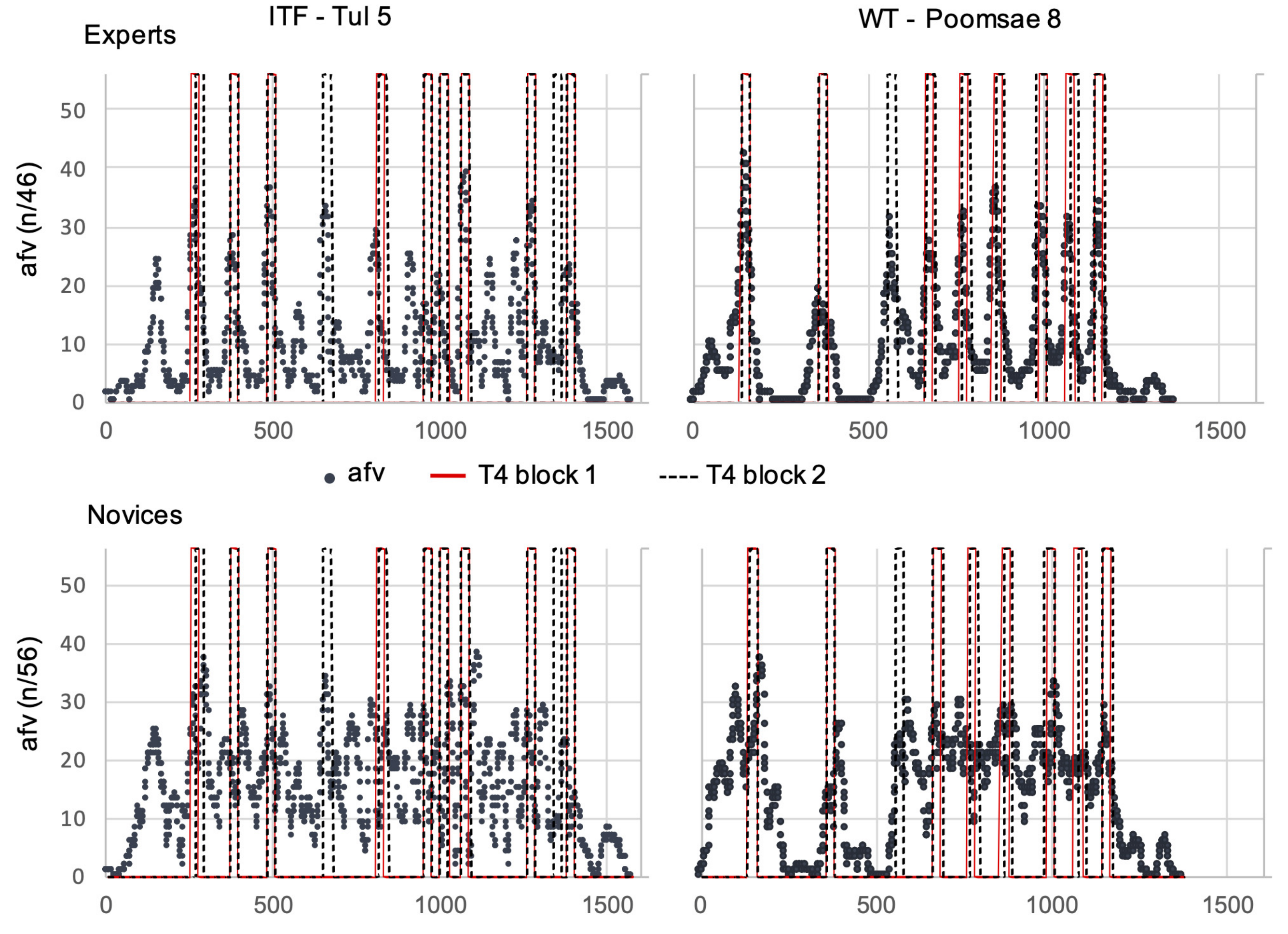

FIGURE 5 | Agreement of within-group responses with boundaries marked by an experienced referee (T4). The added frame values (afv) represent the number of participants responding within each bin (i.e., 1 s prior to each video-frame). Responses of the two blocks are summarized, thus the maximal afv achievable is double the participants in each group (expert group without T4). Red lines represent the boundaries of T4 in block 1, dashed black lines are boundaries from block 2. The exact times of the responses of T4 are at the line marking the end of the 1 s bin during which they are counted (see computation of afv). Two actions, TUL #5 and Poomsae #8, are shown. The complete set of figures for all videos and both groups is provided in **Supplementary Figure 1**. In addition, the two videos with concurrent afv of both groups are provided as **Supplementary Material**.

overlap points to prediction of event boundaries in experts (Schiffer et al., 2015). This was particularly clear in WT sequences of low complexity, where afv peaks in experts are steeper. Notably, 67% of the experts indicated in the questionnaire to have predicted events in time, in contrast to 19% in the control group. For some of the more complex, higher level sequences, the agreement with T4 tended to be reduced. Maxima of novices were sometimes observed in the vicinity of the boundaries marked by T4 but were less well overlapping. This could point to reactive instead of anticipatory boundary detection. However, this speculation requires further evidence.

Further, the comparison with T4 allows some conclusions on the segmentation criteria the experts agreed upon. At the occasion of debriefing T4 indicated that besides using motor simulation he relied on guidelines and regulations of the world federation. Further, he described to segment the sequences in smaller units also during learning. This corresponded to the answers of other athletes.

The complete set of figures for all forms and both groups is provided in **Supplementary Figure 1**. The **Supplementary Videos** allow to observe the relation between agreed boundaries and the movement sequence more directly in a dynamic display. The videos show an animated mark moving through the afv-graphs in synchrony with the movement video. The same videos as those **Figure 5** refers to are shown.

Comparison With Movement Kinematics

Taekwondo form patterns are complex full-body movements for which different body parts are relevant at different times and likely have varying influence on action segmentation over the course of the sequence. To account for this complexity, we chose a procedure in which we selected maxima in acceleration/deceleration using the same approach as for determining agreement between participants. Periods in which values exceeded the mean by 2 SD were marked for each tracked body part separately. For a descriptive comparison, these time windows were graphically overlayed with intervals in which afv was above threshold in the experts and in the novice group (**Figure 6**). Visual inspection revealed that experts' boundaries were occasionally aligned with acceleration maxima or minima of the limbs. As novices had less boundaries there are less occasions

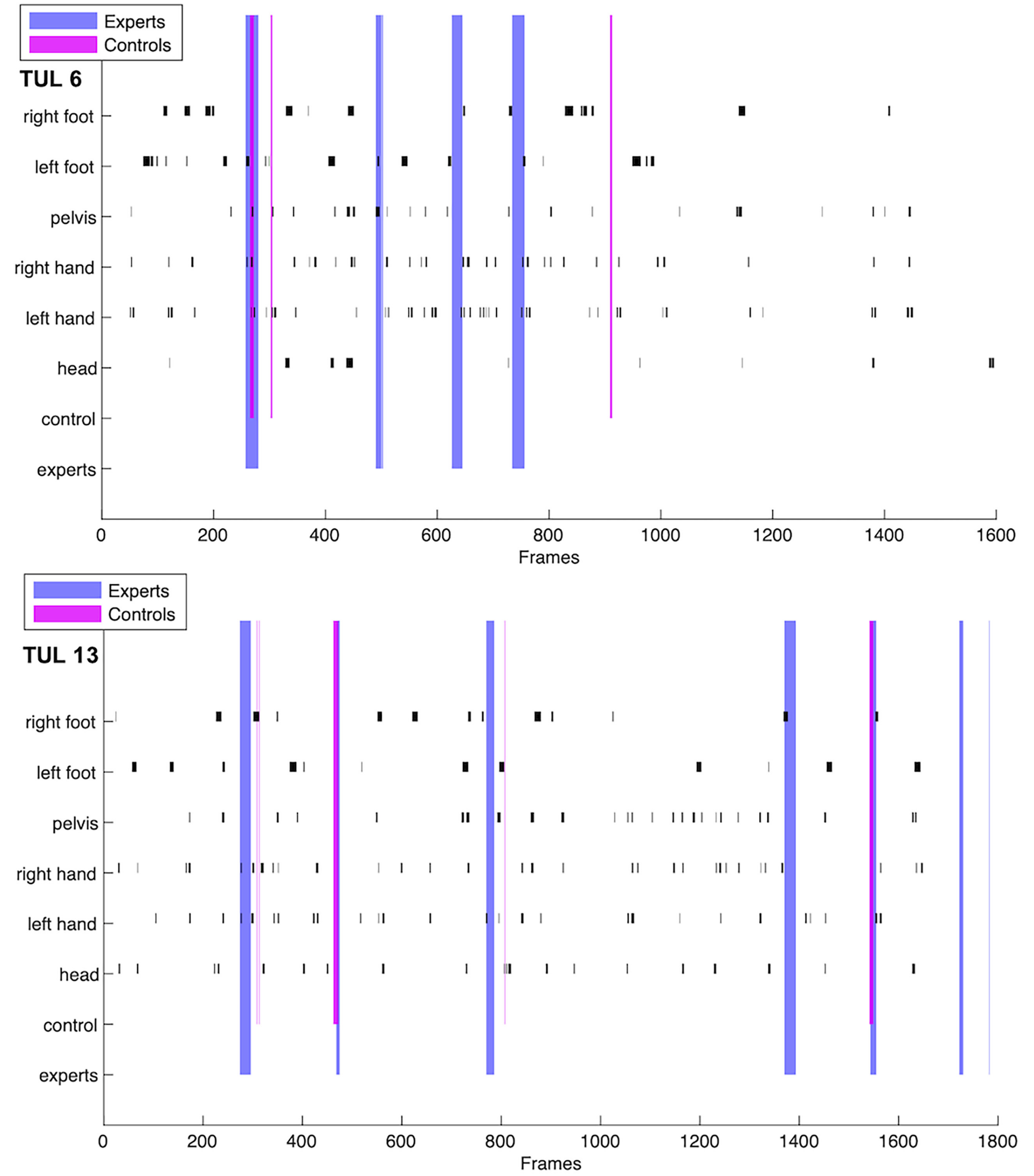

FIGURE 6 | Acceleration maxima (black bars) as obtained for the whole video duration of two ITF sequences (Tul #6 and #13) are shown for six different body parts. Colored lines represent agreed boundaries in the same videos for the two groups (blue – experts; pink – novices, i.e., "controls"). Line width corresponds to length of period in which values were above the mean (i.e., agreed boundaries, n-bound).

for such coincidences and a quantitative comparison between the two groups is unreasonable.

DISCUSSION

The present study aimed to shed lights on shared action representations in Taekwondo experts. Videos showing complex movement sequences of two Taekwondo styles, ITF and WT were presented to participants who were experts in one of these styles or had no experience in martial arts. They provided judgments about the structure of the action sequences by marking boundaries between meaningful units in the observed actions. We measured the within-group agreement on where to mark boundaries and hypothesized that during segmentation experts refer to shared knowledge, resulting in a higher number of agreed boundaries (n-bound). The results confirmed this hypothesis, showing that the group of experts agreed on significantly more boundaries than the novices (**Figure 4**). Remarkably, the experts achieved this level of agreement intuitively, without any explicit instructions about which grain size to apply or which key features they should attend to. As a consequence, there was a remarkable variation in the response frequency in both groups. The number of agreed boundaries was unaffected by Taekwondo style or the complexity of the observed sequences. We assume that different aspects of action representations have influenced segmentation behavior. Besides visuomotor cues in the observed movement, the agreement among experts seems to be based on shared representations about the function of the movement elements and meaningful combinations. The relative roles of these different factors in the context of the segmentation of Taekwondo sequences are discussed.

Within the experimental procedure, several measures were applied to control for confounding effects resulting from basic differences in task understanding, response behavior and strategies between the groups. This included between- and within-subject comparisons of RT in the 0-back control-task and the assessment of intra-individual consistency, represented by the parameter response overlap (ROO). No differences were found between the experts and the control group in these measures. Longer RT in the 0-back control task observed in participants tested in Japan could result from the different equipment used or from different strategies in this task. We found no evidence that this affected other measures.

Grain Size, Observed Movement Kinematics, and Semantic Representations

Zacks et al. (2009) found that participants were guided by the kinematics of arm movements in the context of object manipulation more when they were instructed to do fine grained segmentation. Thus, the grain size of segmentation could be taken as an indicator for the use of visuomotor cues. When segmenting a modern dance piece, novices used smaller grain sizes which increased after amateurs had learned to dance the sequence (Bläsing, 2014). Some members of our control group reported a similar change in strategy with longer time spent on task. Employing videos of basketball games, a recent study (Newberry et al., 2021) found that experts detected more boundaries than novices when they were asked to do fined grained segmentation. This was attributed to their increased visual sensitivity for details (Newberry et al., 2021). However, without instructions that request a particular grain size, we expected experts to mark less boundaries, reflecting their use of semantic knowledge to integrate over longer episodes. In contrast, smaller grain size applied by novices should reflect their use of visuomotor cues. Contrary to these expectations, the grain size did not differ between experts and novices, as expressed in a similar average TBR.

At first glance, the similar average grain size might be taken to suggest that both groups relied on similar representations to segment Taekwondo forms. The observation that experts' boundaries coincided more often speaks against this conclusion. This occurred despite the interindividual variability in TBR was high in both groups and although the average response frequency in experts was not different from that of novices. According to the questionnaire, experts relied on different information than novices (**Table 2**). These different sources are outlined in the following.

In both groups, the response frequency may have been influenced by the inherent structure of Taekwondo forms. In daily actions and also in dance or figure skating which were used in other studies on effects of expertise (Bläsing, 2014; Levine et al., 2017; Di Nota et al., 2020), a comparable structure most likely was not present. Taekwondo sequences consist of accentuated movements of the limbs which represent offensive and defensive techniques, i.e., kicks and blocks toward an imagined opponent. Single elements are frequently separated by changes in movement speed and direction or a change of the performing limb. Further, especially in Poomsae or Tul of lower complexity, the same patterns (i.e., combinations of kicks and blocks) are performed symmetrically to all 4 directions (lateral, forward, and backward). These features establish a temporal structure which could have driven segmentation in both groups, herewith determining the average TBR. In the questionnaire, participants in the control group indicated to have attended to low-level features like tempo, direction changes, and single movements. They used these criteria and combinations of them unsystematically. Some participants reported to have been driven by the rhythmic structure which was specific to the ITF sequences (see **Supplementary Videos**). Attention to the temporal structure of the movement could be reflected in the higher rate of response overlap in ITF observed in novices (**Figure 4**). Experts, in contrast tended to use event prediction and embodied simulation as they imagined how it feels to perform the action.

Semantic representations guided segmentation especially in experts in addition to the sequence structure and to visuomotor cues. As earlier findings on the role of action semantics for segmentation indicate (Levine et al., 2017), mainly experts but also non-experts attend to semantic information such as goal achievement. Here, basic motorcognitive principles such as the preference for action effect coding (Koch et al., 2004; Shin et al., 2010) could be expressed. Beyond basic principles – which special knowledge did Taekwondoists access in addition? The questionnaire pointed to the formation of clusters of elements by experts, comparable to a study by Bläsing (2014). Experts described to rely on higher level semantic representations about meaningful combinations of actions. For instance, knowing that an offense needs to be followed by a defensive movement, experts rarely separated these into different segments. Novices, in contrast, did not seem to adhere to such rules. Although occasionally their marks overlapped with those of experts and even though no differences in grain size were found, the higher n-bound indicates that experts placed boundaries in a more consistent way. The agreement with the responses of T4 is in line with this interpretation and also points to the use of normative criteria. As T4 indicated in the questionnaire, besides employing imagery, he thought of official guidelines for form practice during segmentation. This was not mentioned by any other participant but could have influenced their judgment implicitly. For instance, they would learn about normative criteria during training, such as how high the leg should be raised or whether it should be fully stretched. Another aspect to consider is that T4 and other athletes mentioned to split the sequences into smaller units when they learn them. It is possible, that, at least for familiar sequences, the agreement among athletes is supported by more or less standardized instructions on how to split, i.e., segment the forms.

Generally, temporal alignment reflects prediction of the dynamic action sequence (Schiffer et al., 2015) and likely expert knowledge was beneficial here. For responses to add up in the agreed-boundary-count, it is necessary that individuals time their responses precisely to these segment boarders. Predictive mechanisms were also shown to play a role for the identification of boundaries, as these are characterized as moments when prediction error is high (Eisenberg et al., 2018). These two functions point to predictions on different hierarchical levels of action representation. The temporal alignment of the responses with the observed dynamics might involve sensorimotor processes. The computation of prediction error can also cover larger time spans and may result from semantic action representations. For instance, referring to clustering in experts, prediction error might have been relatively low at the completion of an offensive movement, as they knew that it would be followed by a block. In contrast, in order to place a mark at the end of a leg extension movement, its timing could have been predicted on the basis of sensorimotor expertise. Kinematic and semantic features also coincide, for instance an attack-block combination ends with a decrease in movement speed. This might have caused similar TBR ranges is both groups, even though experts were guided by higher-level semantic and novices by lower-level kinematic features.

Our preliminary analysis in which we overlayed agreed boundaries with the acceleration patterns in six body parts (**Figure 6**) was intended to indicate whether boundaries overlap with the acceleration or deceleration, i.e., kindematics, of arms and legs differentially in both groups. Although it demonstrates descriptively that boundaries and acceleration peaks occasionally coincide, it is not suited for quantitative assessments of group or effector differences. Comparing between groups would be problematic as the frequency of overlaps would be confounded with the lower number of n-bound in novices. An additional difficulty for such an analysis was the complexity of the full body movement, as we outline in the limitations at the end of the discussion.

Role of Familiarity of the Action Sequence

All experts were routined in performing the movement elements (e.g., kicks with hands and feet) but they weren't equally familiar to all action sequences. Moreover, the ITF style was unfamiliar to 19 out of 24 participants. Despite the novelty of half of the sequences, the number of agreed boundaries (n-bound) was equal in both styles and also the level of difficulty had no effect on n-bound in the expert group. Comparing between familiar and unfamiliar sequences in WT athletes only confirmed these results. This points to a transfer of event segmentation to unknown action sequences, at least for this particular type of actions. The findings are in line with a study by Abernethy et al. (2005) who tested the performance in a pattern recall task based on videos of game sequences in experts from three different ball-sports and found that superior performance was to some extent transferred to different ball-sport disciplines (Abernethy et al., 2005). Similarly, studies that employ videos of everyday actions (Zacks et al., 2001; Schubotz et al., 2012) include actions which the observers have not practiced in the same sequences and in a similar context before. Together these results suggest that transfer to unfamiliar sequences is possible as long as these match to the motor repertoire of the observers and are based on known semantic principles. This includes basic principles such as the sensitivity to action goals (Levine et al., 2017). When WT Taekwondo experts segmented unfamiliar ITF forms, the observed actions matched their motor repertoire and, moreover, these known movements were composed according to familiar rules. Conversely, the reason why segmentation was not transferred in dancers who segmented unfamiliar ballet choreographies (Di Nota et al., 2020) could have been the lack of the special motor skills and knowledge of sequence structure required in ballet.

Shared Representations Among Athletes

The generation and structure of shared representations can be explained on the basis of different theoretical frameworks. One explanation is derived from schema theory. With respect to sensorimotor functions, a schema is conceived as the relationship between (1) external conditions, (2) the motor program, (3) the sensory consequences, and (4) the outcomes of the movement (Schmidt, 1975). Repetition during training is thought to strengthen this relationship with the effect that motor programs match expected sensory consequences with increasing precision. Schemata are thought to influence perception and the recall of events. Representations shared among experts might consist of so called "scripts" which are particular schemata describing predictable and frequent action sequences (Rentsch and Davenport, 2006). Different domains in sport vary with regards to which and how many agreed-upon scripts are available or even needed (Rentsch and Davenport, 2006). The technical form discipline of Taekwondo is an example where scripts could be useful due to the stable sequential structure. For the level of agreement Taekwondoists achieved in the present study, it may have been sufficient to rely on scripts with basic rules for the combination of elements. This is derived from the observation that the participants had no experience with at least half of the observed sequences.

A second explanation is based on the cognitive action architecture approach (CAA-A). It describes action representations as integrated networks of movement elements called "basic action concepts" (BACs) (Schack, 2004). Integrating ideas from schema- and ideomotor theories it suggests that BACs are cognitive sets which link representational structures with motor performance, i.e., movements and associated perceptual effects or action goals. In this view, internal action representations are hierarchical tree-like taxonomies of BACs. Motor skill learning re-organizes hierarchies by changing the relations and clusters of BACs (Frank et al., 2015). It was repeatedly shown for experts from different sports, that the representational structure follows a distinct hierarchy which was largely similar between individuals and was in accordance with the functional phases of actions (Schack and Mechsner, 2006; Frank et al., 2015). Comparable to what is found in action segmentation, these studies suggested that in novices interindividual variability is higher and clustering of BACs does not seem to reflect a meaningful organization.

On the background of a dynamic systems approach, a recent review highlighted interpersonal synergies in combat sports (Krabben et al., 2019), suggesting that "a joint perception-action system emerges" (Krabben et al., 2019) where "the perception and action of two individuals are mutually constrained and coupled." According to this concept, the participants in the Taekwondo group of the present study were trained in forming such dynamic synergies with another person, as the majority of them were actively competing in the combat discipline. During a fight, they need to continuously adapt their behavior to that of the opponent. Thus, they are strongly relying on observing with all their senses and predicting their opponents in order to identify advantageous moments to score. About half of the experts practiced forms. Also specialists in the technical form discipline of Taekwondo described to picture an imagined opponent during sequence performance. Irrespective of the specialization of the athletes, experience in representing the opponent might have been beneficial for the agreement in action segmentation. Research on joint action points to a similar direction, proposing that interacting persons need to represent what they can do together (Sebanz et al., 2006; Vesper et al., 2016). These authors highlighted the requirement of representing the interaction itself which goes beyond shared representations of an individual's motor skills or the task set.

Finally, shared representations can be explained from an embodiment perspective. This perspective departs from the view that perception and cognition are grounded in bodily states and sensorimotor processes (Barsalou, 2008) and consequently cannot be thought separately from these. Motor theories of action understanding share this perspective. They assume that the same sensorimotor mechanisms underlie the production and the perception of action (Blakemore and Decety, 2001; Jeannerod, 2001; Wilson and Knoblich, 2005), a notion which has received both behavioral and neural support. Action representations interact with a number of cognitive and perceptual tasks (Rosenbaum et al., 2012). The activation of sensorimotor brain areas during the observation of others' actions, as found in numerous studies (Hardwick et al., 2018), was conceived as "motor resonance" (Uithol et al., 2011). Through this mechanism, shared representations from similar sensorimotor experiences could be activated during observation. This builds a direct link between observed action and the observer's action representations, so called "direct matching" for action understanding. With respect to expertise, direct matching requires some degree of correspondence between the observed action and the observer's repertoire (Wilson, 2001). Support for this requirement was provided from brain imaging studies showing stronger activation in sensorimotor areas of movement experts who observed actions from their domain of expertise (Calvo-Merino et al., 2006; Balser et al., 2014; Cacioppo et al., 2014; Gardner et al., 2015; Apšvalka et al., 2018). Moreover, while observing and predicting skilled actions, experts activated brain representations of the muscles crucial for motor performance (Aglioti et al., 2008). Participants were better at discriminating complex actions when they had learned how to perform them before (Casile and Giese, 2006). Thus, plastic changes that occur in the brain during motor skill learning (Wenger et al., 2017) might change brain processes not only for motor performance but also for perceptual and cognitive tasks (Beilock et al., 2008; Kirsch et al., 2018). In the present study, sensorimotor knowledge achieved through practicing Taekwondo may have contributed to predicting boundaries through an insight into the dynamics and biomechanical constraints. Indeed, about half of the participants from the expert group reported having imagined how it feels to perform the movement (**Table 2**). At this level of action representations, motor resonance presents a framework explaining how shared representations are embodied. In the future, it will be interesting to discuss how embodiment, social embeddedness (Marsh et al., 2009) or a common task or goal (Vesper et al., 2016) can explain shared representations within teams or individual experts in sport at different representational levels.

Limitations and Outlook

This study certainly has a couple of limitations and can be considered preliminary from many perspectives. First, it cannot quantify the relative contributions of the different aspects of action representations, i.e., movement kinematics, basic and expert semantics. The qualitative results provide some insights but the unsystematic and exploratory character of the employed methods has to be admitted. The overlay of the group-wise n-bound with the responses of the expert referee (**Figure 5**) is a descriptive approximation. As long as the criteria behind each of the referees marks are not known exactly, the underlying thoughts can only be derived from more general responses in the questionnaire and, thus, caution is required when interpreting this comparison. Second, we explicitly chose a design which allowed studying implicit agreement but which was not suited to assess the hierarchical organization of action representations (Schack, 2004; Zacks et al., 2009). Third, to test the transfer of segmentation behavior to an unfamiliar style of Taekwondo more systematically, it would have made sense to differentiate between experts in ITF and WT among Taekwondoists to compare the effect of familiarity in a complete cross-over design. Unfortunately, it was not possible to recruit enough ITF athletes for such a comparison. Fourth, as an approach to assess how boundaries are related to movement kinematics, cross-correlations between segmentation patterns and limb acceleration could be computed (Zacks et al., 2009). Ideally, this could reveal temporal relations between the signals to study, for instance, the anticipation of events. This was not doable in the present study, due to the complexity of the movements. A tracked limb was not continuously in use during an entire sequence but different body parts were engaged in alternation. For example, a powerful and fast attack was performed with one leg while the arms were relatively still. This was followed by a fast extension of an arm moving the hand to the front with the feet standing sill and stable on the ground. Consequently, segmentation could have been initially determined by velocity changes of the leg but later in the sequence the contribution of the leg was minimal which would cancel out in a correlation analysis. Future studies might find a way to address the coupling between boundaries and kinematic patterns in complex movement with respect to expertise. Meanwhile, to learn more about the attention to visuomotor cues during segmentation and interactions with expertise, non-periodical movements of a single limb could be tracked with a 3D marker based system instead of video-based tracking. Moreover, segmentation of highly structured actions such as those employed here could be compared to less structured action sequences from Tai-Chi or contemporary dance.

Summary

To summarize, the group of experts agreed on more boundaries than the novices. Taekwondo style and sequence complexity did not significantly modulate this effect. The exact superimposition of the experts' responses in particular bins points to the use of predictive mechanisms based on sensorimotor representations. Prediction on the basis of semantic knowledge might have supported the selection of boundaries. Further, the overlap of the agreed boundaries in the expert group with those of the expert referee suggests that semantic representations and normative aspects were used which Taekwondoists but not novices were familiar with. Due to some limitations, the results can only provide a tentative insight into the content of shared representations.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by the Ethics Committee of Tokyo Metropolitan University (reference number H28-69). The participants provided their written informed consent to participate in this study. Written informed consent was obtained from the individual(s) for the publication of any potentially identifiable images or data included in this article.

AUTHOR CONTRIBUTIONS

WS, JH, and MI conceived the study. VK and WS designed the stimuli and procedure. VK, WS, and MI collected and analyzed the data. RB contributed analyses of movement kinematics. JH provided scientific advice and commented the manuscript. WS wrote the manuscript. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpsyg.2021.733896/full#supplementary-material

Supplementary Videos | To associate the agreed boundaries with the action sequence dynamically, we animated a mark which moves through the afv-graphs in synchrony with the movement video. In this way, the relation between agreed boundaries and the movement sequence might be more directly observable. For each video frame, the afv-graphs indicate how many participants marked a boundary. Peaks show that a high number of participants placed a mark, i.e., a boundary in the action sequence indicating that at the respective moment, a meaningful unit ends and a new one begins. The same videos as used in the movement analysis (**Figure 5**) are provided. The four videos show ITF Tul #5 and WT Poomsae #8, each segmented by experts ($n = 24$) and novices ($n = 28$). The videos display optimally VLC media player software (freeware).

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Epigenetics as a Mechanism of Developmental Embodiment of Stress, Resilience, and Cardiometabolic Risk Across Generations of Latinx Immigrant Families

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Psychosocial stressors can become embodied to alter biology throughout the life course in ways that may have lasting health consequences. Immigrants are particularly vulnerable to high burdens of stress, which have heightened in the current sociopolitical climate. This study is an investigation of how immigration-related stress (IRS) may impact the cardiometabolic risk and epigenetic markers of Latinx immigrant mothers and children in Nashville, TN. We compared stress and resilience factors reported by Latina immigrant mothers and their children (aged 5–13) from two time points spanning the 2016 U.S. presidential election (June 2015–June 2016 baseline, $n = 81$; March–September 2018 follow-up, $n = 39$) with cardiometabolic risk markers (BMI, waist circumference, and blood pressure). We also analyzed these factors in relation to DNA methylation in saliva of stress-related candidate genes (*SLC6A4* and *FKBP5*), generated *via* bisulfite pyrosequencing (complete case n's range from 67–72 baseline and 29–31 follow-up) (n's range from 80 baseline to 36 follow-up). We found various associations with cardiometabolic risk, such as higher social support and greater acculturation were associated with lower BMI in mothers; discrimination and school stress associated with greater waist circumferences in children. Very few exposures associated with *FKBP5*, but various stressors associated with methylation at many sites in *SLC6A4*, including immigrant-related stress in both mothers and children, and fear of parent deportation in children. Additionally, in the mothers, total maternal stress, health stress, and subjective social status associated with methylation at multiple sites of *SLC6A4*. Acculturation associated with methylation in mothers in both genes, though directions of effect varied over time. We also find DNA methylation at *SLC6A4* associates with measures of adiposity and blood pressure, suggesting that methylation may be on the pathway linking stress with cardiometabolic risk. More research is needed to determine the role of these epigenetic differences in contributing to embodiment of stress across generations.

Keywords: epigenetic, embodiment, stress, resilience (psychological), Latinx, maternal and child health, cardiometabolic health

INTRODUCTION

The accumulation of stress over time can contribute to biological embodiment across the life course. Stressors in the early life environment may influence susceptibility to later life chronic disease. Latinx Americans, regardless of immigration status, often experience high rates of chronic stress and are at risk for high rates of cardiometabolic disease later in life, including obesity and hypertension. For example, Latinx adults have 1.65 times the rate of diabetes (1, 2) and 1.2 times the rate of overweight and obesity, relative to non-Latinx whites (3). These health disparities often emerge early in life: overall Latinx children aged 2–19 have 1.6 times the rate of obesity as white children (1), and the youngest group of Latinx children aged 2–5 years have *nearly quadruple* the rates of obesity as white children in the US (4, 5). Currently, immigrants and their US-born children comprise 85.7 million people, which is about 26 percent of the overall US population (6), and nearly half of which report Latinx origins. Thus, Latinx Americans represent an important demographic for the health of the future of the US population.

Latinx immigrant families may be particularly at risk for stress-related diseases, such as cardiometabolic diseases like hypertension and diabetes, as they experience high rates of stressors related to immigrant experiences, including legal status, uncertain immigrant policies, and acculturative stress (7–9). Children of recent immigrants may be at even higher risk than their first-generation immigrant parents, as health outcomes tend to worsen with longer duration in the US, and risk increases across generations, suggesting that racism, xenophobia, or poor living conditions in the US lead to worse health, rather than immigration itself (10–12). Regardless of their own immigrant status, children of Latinx immigrants are disadvantaged on numerous fronts, including access to quality education, health care, and job security for their parents, while being confronted at the same time with resentment, racism, and often violence. Additionally, Latinx children and their parents face heightened stereotypes resulting from recent and highly publicized ongoing debates on immigration policy regarding the Mexican border. These social determinants can affect immigrant families' lifestyles, risk of disease, and mortality. For example, studies find associations between racial discrimination and higher BMI, waist circumference, and blood pressure in young children and in adults (13, 14). While changes in diet and exercise likely contribute to these outcomes, stressors may also become embodied directly through molecular mechanisms that may influence lifetime risk of cardiometabolic disease (15–17).

Embodiment, in this paper, refers to the process by which one's life experiences are literally incorporated biologically, at a molecular level, to influence later life health and disease (18). This process of embodiment is in contrast to the notion of genetic determinism, in which one's phenotype is permanently set by inherited genes. Epigenetic mechanisms, such as DNA methylation, are one process of embodiment by which an individual's phenotype can change over his/her lifetime in response to the environment. The epigenome may be particularly sensitive to embodiment in early life environments, or critical periods, when biological systems are actively being developed (19).

While early life may be the most sensitive period for epigenetic processes, the accumulation of experience over a life course can also alter the epigenome, through potentially environmentally influenced or stochastic changes, as evidenced by identical twins reared apart (20, 21) and aging studies (22–24). When environmentally influenced, epigenetic changes may be a mechanism for the process of weathering, whereby the cumulative effect of social disadvantage over time, such as poverty or discrimination, disproportionately affects the health of disadvantaged populations (25, 26). Regardless of the time period of exposure, the epigenome is clearly sensitive to environmental forces, and has been theorized to help explain the persistence of racial and social health disparities, such as the increased burden of cardiovascular disease among Black relative to white Americans (27), and the higher rates of chronic diseases, such as obesity and diabetes, among Latinos (28). However, as most prior research only examines one time point for epigenetic measures, usually early in childhood, we do not yet know how the epigenome responds to environmental exposures across the lifespan, or how much it contributes to racial disparities in cardiometabolic health.

Most social epigenomic studies to date focus on DNA methylation, which is the addition of a methyl group to the 5′ carbon of a cytosine. Many of these studies tend to use a hypotheses-free genome-wide approach, relying on preselected sites on a microarray, which tend to miss important gene regions (29). Targeted approaches can be useful extensions on this work, when specific hypotheses exist for certain genes, and when working with smaller sample sizes. For example, there are two genes well-established to be involved in the regulation of stress response, including the glucocorticoid receptor chaperone protein gene FK506 Binding protein 5 (*FKBP5*), which is an important regulator of glucocorticoid receptor sensitivity (30, 31) and the serotonin transporter gene (*SLC6A4*), which has been implicated in stress response and increased risk for psychiatric disorders (32). Both genes regulate stress response, and also have a potential role in influencing cardiometabolic risk (15–17).

FKBP5 is a gene known to regulate the glucocorticoid receptor, an important part of the hypothalamic pituitary adrenal (HPA) axis that binds cortisol—an adrenal stress hormone that also regulates metabolism—and thus a good candidate to mediate an epigenetic response to social stress. Many studies have identified associations between adverse childhood experiences, socioeconomic adversity, and other environmental stressors with lower DNA methylation of *FKBP5* across various tissues as reviewed in Parade et al. (33). Demethylation of intron 2 of *FKBP5* has been shown to disrupt the HPA axis and contribute to glucocorticoid resistance, higher cortisol levels, and prolonged recovery following exposure to stress (34). One study of maternal-neonatal pairs in the Democratic Republic of Congo found significant methylation changes at different transcription factor binding sites in *FKBP5*, along with other HPA axis related genes, in association with chronic stress and war trauma across maternal blood, placenta, and newborn cord blood (35). Decreased methylation at *FKBP5* has also been identified in blood cells of adults who had experienced childhood trauma (36), in blood cells of Holocaust survivors with Post-Traumatic Stress Disorder (PTSD) and their offspring (37), and in buccal epithelial cells of adolescents who experienced early-life institutionalization in Romania (38). One study found methylation in one site of *FKBP5* was a predictor of both PTSD symptom severity and resilience (in opposite directions) in saliva (39). However, a different study found an opposite direction of effect in saliva, such that stress in childhood was associated with *higher* methylation of this gene in young adulthood (40), and a number of studies found no associations between childhood adversity and methylation at this gene (41–43) (though methylation and expression of this gene were usually linked with higher rates of depression) (41, 42). Higher methylation at this gene has also been linked with less healthy metabolic measures, such as waist circumference (15). While there is some inconsistency in findings, the majority of studies observed significant associations of child adversity and methylation across tissues, suggesting systemwide effects of early adversity on methylation at this gene, which may have relevance for cardiometabolic risk.

SLC6A4 is a second gene with well-established associations with maternal care, early life adversity, and long-term child development. This gene is involved in serotonin and dopamine releases and has been implicated in stress response and increased risk for psychiatric disorders (44). *SLC6A4* helps regulate the bioavailability of serotonin and thus modulates mood, anxiety, and energy homeostasis. The majority of studies investigating this gene found that the 5-HTTLPR genotype moderates the relationship between early life stress and depression (45, 46). A growing number of studies have also found DNA methylation in the promoter of this gene in blood to be positively associated with child adversities (47–50), though in contrast one study found *decreased* promoter methylation in maternal and cord blood associated with depression in pregnancy (51). Methylation at *SLC6A4* also has been related to cardiometabolic health, as one study found promoter hypermethylation in blood leukocytes to be significantly associated with an increased prevalence of obesity (16). Altered methylation of CpG5 in cord blood was also found to be associated with greater concurrent measures of adiposity including BMI and waist circumference (17).

Latinx immigrant families in the US are living in a state of chronic stress, constantly on edge with concerns about deportation of their family members, or their ability to remain in the country in which most of them have lived for the majority of their lives, particularly in the years since the 2016 Presidential election. The epigenetic effects of increasing stress and anxiety associated with this particular sociopolitical moment for Latinx families are yet to be studied. To our knowledge, only one other study, completed in 2010, has investigated associations between discrimination and DNA methylation in Latina women (52). In blood from 147 pregnant Latina women, they identified decreased methylation in *FKBP5* associated with increased discrimination over time, though not always in expected directions. Only our prior study has investigated epigenetics of children of immigrants in relation to multiple psychosocial stress and resilience factors (53). We generally found increased stress and decreased social support associated with decreased epigenetic age, suggesting stress may slow child development. Few other studies have examined epigenetics of social support or any other positive social factor.

Study Purpose and Hypotheses

The current study examined associations between psychosocial stressors and resilience factors with cardiometabolic risk factors, along with targeted DNA methylation in the *FKBP5* and *SLC6A4* genes in saliva of Latina immigrant mothers and their children. This study represents a targeted extension of our previous genome-wide analysis of the children's samples (53). We hypothesized that stressors measured both in childhood and adulthood would be associated with cardiometabolic markers including higher BMI, waist circumference, and blood pressure. We further predicted that stressors would associate with decreased DNA methylation at key CpG sites within intron 2 of *FKBP5,* and with increased methylation of the promoter region of *SLC6A4*. Finally, we predicted that methylation at these genes may associate with cardiometabolic markers. Overall, this study may be the first to examine repeated epigenetic and cardiometabolic measures in relation to stress and resilience within a longitudinal sample of Latina immigrant mothers and their children.

MATERIALS AND METHODS

Study Population

The study sample draws from a longitudinal study of stress embodiment, entitled "Children of Hispanic Immigrants Collaborating to Overcome Stress" (CHICOS). The study recruited 81 families (mother-child dyads) in Nashville, TN between June 2015 and June 2016. This initial time point is called "baseline" throughout the rest of the study. Participants were recruited from local immigrant-serving community centers with subsequent snowball sampling. Inclusion criteria were self-described Latina, foreign-born immigrant mothers above age 18, with a child between the ages of 5–13. The mother and focal child were assessed on a number of different biological, psychosocial, and health-related measures. Following baseline assessment of the dyads, we revisited the same families 2–3 years later (March–September 2018), collecting the same data and new interviews focused on changes since the 2016 presidential election, from all available mothers and children who participated in the baseline sample ($n = 39$). This time point is referred to as "follow-up" throughout the study. Informed oral consent was provided by all participants, and Vanderbilt University and University of California San Diego Institutional Review Boards approved all protocols. All data are available upon request, and key measures are available in **Supplementary Table 4.0**.

Exposures: Psychosocial Stressors and Resilience Factors

All exposure data were collected using surveys administered in person with mothers in Spanish (1.5–2 h) and children primarily in English (45 min). Surveys were a combination of validated scales and new survey questions developed following a set of preliminary individual interviews in 2014 with children, and focus groups with Latina immigrant mothers in Nashville, TN (54). Questions included in each scale are described in brief below, and detailed further elsewhere (53).

Psychosocial Stressors

Multiple measures of psychosocial stress were assessed, covering a range of domains, and including maternal and child assessment of each domain. Measures reported at both time points separately by children and mothers included *immigrant-related stress (IRS), discrimination stress,* and a *total stress score*. Measures additionally reported by only mothers included *family economic stress, family health stress,* and *household stress*. A measure reported only by the children was *school stress*. The questions included in each stress scale and Cronbach's alpha score for internal reliability are available elsewhere (53). The validated e*veryday discrimination* scale was also reported separately for mothers and children at the follow-up time point (55). This scale has been validated in Latina adults (56). All indices were calculated by taking the mean of responses for those not missing more than two questions, and higher scores indicate more stress across all measures. Outside of the scales, we also examined one individual question about the *child's fear of parent deportation.*

Resilience Measures

Measures of resilience included *social support* and *optimism* reported separately by mothers and children. We developed child-focused social support questions focusing on support from the parents (53). Social support and social connection in mothers were measured with a modified index from the Berkman Syme Social Network Index (57). Generalized dispositional optimism was measured in the mothers using the revised 10-item version of the Life Orientation Test (58), a scale which has been validated in Latina adults (59). To measure optimism in the children, we used the Y-LOT, the youth version of the LOT-R, which has been validated in a racially diverse set of 3rd to 6th grade children (60). Y-LOT was only measured at follow-up.

A measure of *subjective social status* (SSS) was also considered a resilience factor, as higher scores indicate better social standing. SSS has been linked with self-reported health among immigrant Latinas, and has been hypothesized to capture immigrant experiences that may alter perceived self-worth (61). Maternal SSS was measured at baseline and follow-up time points with the MacArthur SSS scale, which asks mothers to report where they felt they fit on a social ladder (range 1–10) in relation to others in the US (62). This scale has been validated and demonstrated reliability among diverse racial/ethnic groups, including Latinas (63). We also used the language use subscale of the Short Acculturation Scale for Hispanics (SASH), which has shown to be highly correlated with the overall SASH scale in validation studies (64).

Outcomes: Cardiometabolic Biomarkers and DNA Methylation

Cardiometabolic Biomarkers

Multiple measures of cardiometabolic risk were assessed in both the children and the mothers at both time points. In the children, we measured adiposity with Body Mass Index (BMI) percentile (adjusted for child age and gender) and waist circumference. In the mothers, we measured BMI, systolic blood pressure (SBP), and diastolic blood pressure (DBP).

DNA Methylation

Genomic DNA was extracted from 79 Oragene saliva samples from children in 2015–2016 and again in 2018 (38 samples) using standard protocols (DNA Genotek, Ottawa, Ontario, Canada). Genomic DNA was also extracted from saliva of 80 mothers at baseline and 40 mothers in follow-up. Saliva was stored at room temperature, per manufacturer's recommendation until DNA extraction. DNA was isolated from 500 μl of children's saliva using prepIT-L2P (Zymo Research, CA, USA) and stored at −20°C until time of analysis. DNA was excluded from four child samples at baseline and one child and two maternal samples collected follow-up due to low quality/concentration of DNA, as measured by Nanodrop and Qubit. The level of DNA methylation was assessed *via* bisulfite pyrosequencing at two CpG sites within intron 7 of the *FKBP5* gene and six sites within the promoter region of the *SLC6A4* gene. In the end, we generated high quality methylation data from 78 child and maternal samples at baseline and 36 child and 38 maternal samples at follow-up for *FKBP5*. For *SLC6A4*, we generated data for 78 child and 80 maternal samples at baseline and 37 samples for both groups at follow-up. These gene regions were chosen based on prior studies highlighting their importance in early life adversity in humans, other primates, and rodents (38, 65, 66). These specific CpG sites assayed were in important regulatory regions, including the glucocorticoid response element of intron 7 of *FKBP5*, and the promoter region of *SLC6A4*. Primers for *FKBP5* were designed by EpigenDx (Assay ADS3828-FS2), which covers two sites in Bin 2 of intron 7 (37). Specific primer information of these gene regions can be found in **Supplementary Table 2.0**.

In brief, 500 ng of DNA from each sample was bisulfite converted in duplicate using the EZ DNA Methylation Gold Kit (Zymo Research, CA), according to manufacturer's protocol. Duplicate bisulfite-converted DNA was mixed with 0.2 μM of each primer and amplified using the HotstarTaq plus Master Mix (Qiagen, CA). For each sample, PCRs were performed on each of the duplicate bisulfite treatments using the following protocol for *SLC6A4* gene: one cycle of 95°C for 5 min, 45 cycles of 94°C for 1 min, 58°C for 1 min, 72°C for 1 min, and 72° for 10 min. For *FKBP5* gene: one cycle of 95°C for 5 min, 45 cycles of 95°C for 30 s, 56°C for 30 s, 72°C for 30 s, and 68° for 10 min.

DNA methylation levels for all CpG sites were assessed using the Pyromark Q24 pyrosequencer, following standard protocols (Qiagen, CA). A bisulfite conversion check was included in each assay to verify full conversion of the DNA. If the difference between two bisulfite replicates exceeded two standard deviations (SDs) of the variation in the entire study population, a third bisulfite treatment was tested and the average of the two closest results was used. The final analytical sample with complete data at baseline for children ranged from 67 to 68, and for mothers $n = 72$, and follow-up children's sample $n = 29$–31, and mother's sample $n = 30$–31.

Covariates

Mothers self-reported at each time point their own age, marital status, number of years lived in the US, legal status, and maternal smoking status. Children reported their own age and gender at each time point.

Data Analyses

We first tested correlations between each psychosocial stressor and resilience factor, key demographic factors, and all measures of cardiometabolic risk, and DNA methylation across all studied sites of *SLC6A4* and *FKBP5,* separately at each time point, using Pearson's correlations, to guide model building in subsequent analyses.

We next modeled associations between each psychosocial stressor and resilience factor with all cardiometabolic risk markers, and separately with each methylation site, and the average across sites, in the two genes. While a formal mediation analyses was not supported by our small sample size, we also tested if the methylation levels at any site within either gene were associated with the cardiometabolic risk markers to test the hypothesis that methylation of stress-related genes may be on the pathway toward cardiometabolic disease.

All associations were modeled using linear regressions by adjusting for a set of key covariates, including child's age, mother's age, child's gender, and maternal smoking, which are known confounders in epigenetic studies (67). All associations are presented as Beta estimate (standard deviation), *p*-value. We tested additionally including socioeconomic and immigrant-related demographic factors, including maternal years in the US, legal status, marital status, and education level, but missing data across variables limited the value of these models, which are not presented. Where significant, we also report the effects of each of these factors given their role in contributing to the immigrant context. We chose not to adjust for multiple testing corrections, since these adjustments can be overly conservative for exploratory analyses, particularly when methylation sites are highly correlated within regions, and exposures are also correlated. All analyses were conducted in R (http://www.R-project.org).

In a secondary set of analyses, we examined differences in methylation levels over time in both mothers and children, as well as the overall relationship between mothers and children's methylation at each time point using paired *t*-tests. We also explored longitudinal changes in methylation with linear mixed models, adjusting for the same key demographics as other described models.

RESULTS

Demographics

Population Characteristics

Demographic characteristics of our analytical sample of 79 baseline and 39 follow-up CHICOS participant mothers and children are displayed in **Table 1**. In brief, at baseline, mean age of children was 8.7 years, 56% female, and the majority were born in the US (72%). Mothers were mean age 34.6 years, primarily non-smokers (97.4%), mostly born in Mexico (86.8%), lived in the US on average 12.6 years, and majority self-reported undocumented (85.3%). Mothers were mostly married (85.5%) and with few years of education (mean 9 years), and over a third had trouble paying basic bills (39.5%). In comparing demographics of analyzed subjects vs. those lost to follow-up, we found those lost were significantly more likely to be undocumented and unmarried mothers at baseline, but did not differ in other measured demographics.

Stress and Resilience Levels

All measured stress and resilience levels at both time points are reported in **Table 1**. Generally, we found stress levels in mothers were high across both time points, with slight decreases in total stress and immigrant stress over time, while resilience factors such as optimism and social support also decreased over time. In children, stress and resilience measures both generally increased over time, particularly immigrant stress and social support from parents. There was wide variation across most of these measures in this sample, as reported previously (53).

Correlations Among All Study Variables

Bivariate correlations between all study variables can be found in **Supplementary Tables 3.0, 3.1, 4.0, 4.1**. In brief, many correlations were found in expected directions between stress and resilience exposures with cardiometabolic risk factors and DNA methylation in both mothers and children, though results varied somewhat across generations and across time points. These exploratory analyses guided the building of linear models, which showed largely similar results, as described below.

Associations Between Stressors and Cardiometabolic Markers

In linear models adjusted for key covariates at baseline, no variables associated with children's cardiometabolic markers, but in mothers, social support and connection inversely associated with BMI [Beta: −2.15 (SD < 0.01), $p = 0.034$] (**Table 2**). At follow-up, children's school stress [B: 22.15 (10.72), $p = 0.048$] and everyday discrimination [B: 9.92 (3.72), $p = 0.015$] were positively associated with children's waist circumference. In the mothers at follow-up, a negative association was detected between acculturation (SASH) and BMI [B= −2.96 (1.44), $p = 0.049$], and between subjective social status and SBP [B: −2.71 (1.27), $p = 0.040$] (**Table 2**). Other marginal associations are displayed in **Table 2**.

Associations Between Stress/Resilience and *FKBP5* Methylation

At baseline in children, only the variables of fear of parent's deportation and everyday discrimination were marginally associated with *FKBP5* methylation (**Table 3**). In mothers at baseline, a significant negative association was found between mother's acculturation (SASH) and mother's *FKBP5* methylation, such that those who communicated more comfortably in English had lower methylation at the first CpG site [B: −1.19 (0.44), $p = 0.008$] and lower average methylation across sites of *FKBP5* [B: −0.89 (0.36), $p = 0.017$; **Table 3**].

TABLE 1 | Demographics, social stressors, and resilience factors over time, complete case data.

	Baseline ($n = 79$) *n*, % or mean (sd, range)	**Follow-up ($n = 39$) *n*, % or mean (sd, range)**	**Missing data baseline/follow-up**	***p*-value†**
Child demographics				
Age in years	8.67 (2.13, 5–13)	10.5 (2.10, 6–15)	1/2	**<0.001**
Gender (female)	44 (56.4%)	17 (47.2%)	1/1	–
Country of birth			0/2	–
United States	57 (72.2%)	27 (73.0%)		
Other	22 (27.8%)	10 (27.0%)		
Mother demographics				
Age in years	34.61 (5.95, 23–52)	37.45 (4.84, 29–47)	3/0	**<0.001**
Country of birth			3/1	–
Mexico	66 (86.8%)	35 (92.1%)		
Other Latinx country	10 (13.2%)	3 (7.9%)		
Years in US	12.59 (3.97, 4–27)	14.98 (3.46, 6.67–22.42)	4/2	**<0.001**
Legal status			4/3	**<0.001**
Undocumented	64 (85.3%)	33 (91.7%)		
Documented	11 (14.7%)	3 (8.3%)		
Marital status			3/1	**0.041**
Married	65 (85.5%)	29 (76.3%)		
Single	11 (14.5%)	9 (23.7%)		
Years of education	9.39 (3.18, 2–18)	9.57 (3.24, 2–16)	3/1	–
Trouble paying basic bills (yes)	30 (39.5%)	10 (27.0%)	3/2	0.228
Smoking frequency	2 (2.6%)	3 (7.9%)	3/1	0.617
Child psychosocial stressors				
Total child stress (0–2)	0.56 (0.26, 0.13–1.31)	0.43 (0.15, 0.12–0.75)	4/5	0.196
Immigrant stress score (0–2)	0.85 (0.38, 0–1.75)	0.99 (0.38, 0.2–1.8)	2/3	**0.009**
Discrimination stress (0–2)	0.27 (0.37, 0–2)	0.21 (0.31, 0–1.4)	2/3	0.482
School-related stress (0–2)	0.51 (0.32, 0–1.43)	0.55 (0.28, 0–1.43)	3/4	0.126
Fear of parent's deportation			2/3	*0.085*
Never	27 (35.0%)	8 (22.2%)		
Sometimes	31 (40.3%)	19 (52.8%)		
Always	19 (24.7%)	9 (25%)		
Child resilience factors				
Social support parents (0–2)	1.41 (0.41, 0.5–2.0)	1.53 (0.34, 0.6–2.0)	2/3	**0.002**
Optimism (YLOT; 12–48)	–	32.83 (7.08, 20–46)	39/3	–
Mother report of psychosocial stressors				
Total maternal stress (0–1)	0.30 (0.17, 0.02–0.78)	0.25 (0.12, 0.02–0.53)	8/5	**0.019**
Immigrant stress score (0–1)	0.46 (0.23, 0–0.9)	0.42 (0.21, 0–0.8)	8/1	**0.002**
Discrimination score (0–1)	0.43 (0.25, 0–1.0)	0.36 (0.24, 0–0.86)	6/2	*0.053*
Household stress (0–1)	0.21 (0.21, 0.0–0.8)	0.23 (0.20, 0.0–0.8)	5/1	0.610
Family economic stress (0–1)	0.24 (0.24, 0.0–1.0)	0.17 (0.17, 0.0–0.63)	6/4	*0.059*
Health stress (0–1)	0.32 (0.26, 0.0–1.0)	0.27 (0.22, 0.0–1.0)	3/2	0.224
Mother resilience variables				
Subjective social status (1–10)	4.07 (1.88, 1–9)	4.32 (1.56, 1–8)	3/1	*0.075*
Social support and connection (1–4)	2.48 (0.58, 0.25–3.40)	2.19 (0.56, 1.0–3.40)	3/1	**0.019**
Optimism (0–24)	17.12 (3.05, 12–24)	13.66 (2.30, 8–18)	5/1	**<0.001**

†*P-value based on paired t-tests for continuous variables, and McNemar (paired Chi Square) test for categorical variables. Comparisons were calculated only on the 36 individuals in both time points. Bolded values represent significant associations. Italicized values represent marginal associations. Values in parentheses following psychosocial stressors and resilience factors represent the potential range of each measure.*

TABLE 2 | Children's and Mothers' psychosocial stressors, resilience factors, and cardiometabolic biomarkers.

	Children's cardiometabolic health biomarkers		
	BMI percentile B (SD)	**Waist circumference B (SD)**	
Children's measures at follow-up	*n* = 31	*n* = 30	
Stress variables			
Total child stress score	–	*42.13 (21.09)*	
School stress	–	**22.15 (10.72)**	
Everyday discrimination	–	**9.92 (3.72)**	
Discrimination stress	–	*20.16 (10.88)*	
	Mother's cardiometabolic health biomarkers		
	BMI B (SD)	**SBP B (SD)**	**DBP B (SD)**
Mothers' measures at baseline	*n* = 76	*n* = 73	*n* = 73
Stress factors:			
Immigrant related stress	–	*12.04 (6.57)*	–
Discrimination stress	–	*10.92 (6.29)*	–
Resilience factors:			
Social support/social connection	**−2.15 (<0.01)**	–	–
Optimism	*−0.34 (0.20)*	–	*0.59 (0.35)*
Mothers' measures at follow-up	*n* = 30	*n* = 34	*n* = 34
Stress factors:			
Discrimination stress	–	*15.8 (8.37)*	–
Resilience factors:			
Subjective Social Status	–	**−2.71 (1.27)**	–
Social support/social connection	–	–	*5.11 (2.87)*
Acculturation (SASH)	**−2.96 (1.44)**	–	–

B, Beta, represents unstandardized regression coefficients; SD, standard deviation. Only significant (bolded) or marginalized (italicized) findings are presented.

TABLE 3 | Psychosocial stressors and resilience factors and methylation levels at *FKBP5* of children and mothers at both time points.

	FKBP5		
Baseline	**CpG1**	**CpG2**	**Average**
Child stress variables	**B (SD)**	**B (SD)**	**B (SD)**
Fear of parent's deportation	–	*0.72 (0.37)*	–
Discrimination stress	*−1.93 (1.06)*	–	–
Maternal resilience variables			
Acculturation (SASH)	**−1.19 (0.44)**	*−0.58 (0.33)*	**−0.89 (0.36)**
Follow-up	**CpG1**	**CpG2**	**Average**
Child stress variables			
Everyday discrimination	–	**−1.03 (0.38)**	*−0.93 (0.45)*
Child resilience variables:			
Parental social support	**2.86 (1.29)**	–	*1.94 (1.07)*
Maternal stress variables:			
Family health stress	–	–	*−1.25 (0.64)*

B, Beta, represents unstandardized regression coefficients; SD, standard deviation. Only significant (bolded) or marginalized (italicized) findings are presented.

At follow-up, a negative association was found between child's report of Everyday Discrimination and children's methylation at the second site of *FKBP5* [B: −1.03 (0.38), $p = 0.0141$]. Child's report of parental social support was positively associated with methylation at the first site [B: 2.86 (1.29), $p = 0.035$] of *FKBP5* (**Table 3**).

Associations Between Stress/Resilience and *SLC6A4* Methylation

In children at baseline, positive associations were detected between IRS with two sites in *SLC6A4*: CpG3 and CpG5 (**Table 4**). Children's fear of parent's deportation was also associated with CpG sites 3, 5, and 6 of *SLC6A4* (all $p < 0.040$). In mothers at baseline, various sites of *SLC6A4* were positively associated with total maternal stress, IRS, health stress, and discrimination stress (**Table 4**, all $p < 0.040$). SSS was negatively associated with CpG1, CpG3, CpG6, and average methylation (all $p < 0.030$).

In children at follow-up, optimism was negatively associated with CpG2 in *SLC6A4* [B: −0.07 (0.03), $p = 0.040$] (**Table 4**). In mothers we see some associations in the opposite direction as seen at baseline, as both IRS and household stress *negatively* associated with CpG4 of *SLC6A4* (all $p < 0.02$), while SASH was *positively* associated with CpG3, CpG4, CpG5, and average methylation at *SLC6A4* (**Table 4**).

Associations Between Methylation and Cardiometabolic Markers

In the children at baseline, we detected significant inverse associations at baseline between several sites and the average

TABLE 4 | Psychosocial stressors and resilience factors and methylation levels at *SLC6A4* of children and mothers at both time points.

	SLC6A4						
	CpG1	**CpG2**	**CpG3**	**CpG4**	**CpG5**	**CpG6**	**Average**
Baseline							
Child variables	**B (SD)**	**B (SD)**	**B (SD)**	**B (SD)**	**B (SD)**	**B (SD)**	**B (SD)**
Stress factors:							
Total stress score	–	–	–	–	*0.98 (0.67)*	*1.34 (0.68)*	–
School stress	–	–	–	*0.73 (0.47)*	*0.78 (0.53)*	–	–
Immigrant-related stress	–	–	**0.77 (0.35)**	–	**0.89 (0.44)**	*0.89 (0.45)*	–
Fear of parent's deportation	–	–	**0.38 (0.17)**	*0.34 (0.19)*	**0.55 (0.21)**	**0.49 (0.21)**	*0.25 (0.15)*
Maternal variables							
Stress factors:							
Total stress score	*2.72 (1.37)*	1.85 (1.19)	*2.17 (1.20)*	–	–	**2.10 (0.93)**	**1.50 (0.70)**
Immigrant-related stress	**2.74 (0.98)**	**1.83 (0.85)**	**2.11 (0.86)**	–	–	**1.65 (0.67)**	**1.56 (0.49)**
Family health stress	–	–	**1.92 (0.76)**	–	–	**1.50 (0.60)**	**0.94 (0.45)**
Discrimination stress	**1.98 (0.95)**	–	–	–	–	–	**1.01 (0.49)**
Resilience factors:							
Subjective social status	**−0.25 (0.12)**	–	**−0.23 (0.10)**	*−0.13 (0.08)*	−0.02 (0.06)	**−0.24 (0.08)**	**−0.17 (0.06)**
Acculturation (SASH)	*−0.88 (0.44)*	–	–	–	–	–	–
Follow-up							
Child variables							
Resilience factors:							
Parental social support	–	*−1.21 (0.65)*	–	–	–	–	–
Optimism	**–**	**−0.07 (0.03)**	–	–	–	–	–
Maternal variables							
Stress factors:							
Immigrant-related stress	–	–	–	**−3.37 (1.30)**	–	–	–
Household stress	**–**	–	–	**−2.64 (0.99)**	–	–	–
Resilience factors:							
Acculturation (SASH)	–	*−0.51 (0.25)*	**0.54 (0.23)**	**0.84 (0.27)**	**0.61 (0.29)**	–	**0.61 (0.22)**

B, Beta, represents unstandardized regression coefficients; SD, standard deviation. Only significant (bolded) or marginalized (italicized) findings are presented.

methylation of *SLC6A4* with both BMI percentile and waist circumference (**Table 5**). Associations were consistently in the negative direction in the smaller sample size at follow-up, though not significant (data not shown). In the mothers at follow-up, we detected positive associations between multiple sites of *SLC6A4* and DBP—but not with SBP or BMI (**Table 5**).

Secondary Analyses: Cross-Generational and Longitudinal Analyses

Comparing Methylation Across Generations: Mothers vs. Children

At the baseline timepoint, paired t-tests revealed no significant differences between mothers and children across sites of *FKBP5*, though mothers tended to show lower methylation than children at CpG1 and the average. Mother's DNA methylation was significantly higher relative to the child's methylation in *SLC6A4* average and at sites CpG1, CpG2, and CpG4, (all $p < 0.005$, **Supplementary Figure 1.0**). At the follow-up time point, the mother's methylation was significantly higher than the child's at *SLC6A4* CpG4 ($t = 2.41$, df $= 34$, $p = 0.022$; **Supplementary Figure 1.1**).

Longitudinal Analyses

Children showed a significant increase over time in *SLC6A4* methylation at CpG1 ($t = 2.15$, df $= 34$, $p = 0.039$). Mothers showed a significant decrease in *FKBP5* methylation at CpG2 site ($t = -2.86$, df $= 23$, $p = 0.009$) and average across sites ($t = -2.14$, df $= 23$, $p = 0.0430$) (**Supplementary Figure 2.0**). We found the same site of CpG1 in *SLC6A4* in children to show significant change over time in a linear mixed model, after adjusting for key demographic covariates, suggesting that the methylation change was independent of age (and age was not significantly associated). For maternal methylation, no significant changes over time were detected for *FKBP5* after adjusting for covariates.

TABLE 5 | Children's and mothers' SLC6A4 methylation levels and cardiometabolic biomarkers.

	Child's BMI percentile at baseline	*p*-value	Child's waist circumference at baseline	*p*-value	Mother's DBP at follow-up	*p*-value
	***n* = 69**		***n* = 62**		***n* = 32**	
	B (SD)		**B (SD)**		**B (SD)**	
SLC6A4						
Average	**−11.75 (3.63)**	**0.002**	**−4.63 (1.54)**	**0.004**	**4.10 (1.61)**	**0.016**
CpG 1	**−3.91 (1.73)**	**0.027**	**−2.00 (0.71)**	**0.007**	–	–
CpG 2	–	–	*−2.49 (1.39)*	*0.078*	**3.46 (1.49)**	**0.027**
CpG 3	*−6.01 (3.27)*	*0.070*	**−2.91 (1.34)**	**0.033**	**3.64 (1.62)**	**0.032**
CpG 4	*−5.84 (2.95)*	*0.052*	–	–	**3.55 (1.24)**	**0.007**
CpG 5	**−5.94 (2.60)**	**0.025**	**−2.24 (1.08)**	**0.042**	**3.28 (1.23)**	**0.012**
CpG 6	**−7.00 (2.52)**	**0.007**	*−2.12 (1.20)*	*0.082*	**2.52 (1.15)**	**0.036**

B, Beta, represents unstandardized regression coefficients; SD, standard deviation. Only significant (bolded) or marginalized (italicized) findings are presented.

DISCUSSION

This study is the first, to our knowledge, to demonstrate the impact of daily stressors of immigrant families (mothers and children) on cardiometabolic risk and DNA methylation of stress-related genes over time. In general, stressors were associated with increased adiposity, while protective factors, such as social support and higher subjective social status were negatively associated with adiposity and BP. Associations with epigenetic factors were generally in the expected direction in both mothers and children within each gene, such that increased levels of stress were associated with higher DNA methylation in *SLC6A4,* and greater levels of resilience factors were associated with lower methylation. While fewer associations were detected with *FKBP5*, generally, greater stress was associated with lower DNA methylation, and greater resilience with higher methylation. These trends were consistent with prior studies of these gene regions, where greater stress was associated with higher methylation in the promoter of *SLC6A4*, and lower methylation in intron 7 of *FKBP5* (37, 38).

Below we describe in detail the magnitude and directions of associations, how our results relate to similar studies and contribute to theories of embodiment across the life course, and the potential functional relevance of findings.

Embodiment via Cardiometabolic Risk Measures

We found children's stressors, such as everyday discrimination and school stress, positively associated with larger waist circumferences. This trend is consistent with other studies in adults that have shown stressors such as everyday discrimination to be associated with increased waist circumference (14) and low socioeconomic status to be related to greater abdominal fat deposit (68). In one study of Australian children (mean age 11 years), racial discrimination was associated with increased BMI, waist circumference, and SBP (14). A meta-analysis has documented strong associations between increased maternal stress and greater obesity in children (69), though fewer studies have measured stress experienced directly by children. Our data suggest that increased risk for obesity may be influenced by stress experienced by children in early to mid-childhood, even earlier in life than usually studied. This finding suggests the importance for health care providers to consider monitoring children's psychosocial stressors as contributors to cardiometabolic risk early in life, in order to curb progression of largely preventable cardiometabolic diseases.

In the mothers, we found greater acculturation and resilience factors (e.g., higher subjective social status, higher social support), associated with lower cardiometabolic risk, but little evidence that stress associated with either BMI or BP. A substantial literature supports associations between social support and BP and BMI; e.g., social support has been associated with lower BP reactivity to laboratory stress in older adults (70) and was protective against intergenerational transmission of obesity in a study of Finns in mid-adulthood (71). Findings with acculturation are more mixed. A systematic review found inconsistent effects of acculturation on BMI, such that 3 studies were consistent with our finding of lower BMI with more acculturation (which were mainly among women), while 6 studies of mixed gender showed the opposite pattern (72). BMI can be influenced by many complex factors, including cultural norms for body image, food availability, physical activity norms, and loss of a "healthy migrant effect" over time, such that it is challenging to predict how acculturation may influence this trait. Further research is needed to determine how acculturation and other resilience factors can protect against elevated cardiometabolic risk, to reduce the risk of multiple preventable health outcomes, including hypertension, diabetes, stroke, and overall mortality (73).

HPA axis dysregulation may be a mediating factor between psychosocial stress and increased risk of cardiometabolic disease. Many studies have found chronic stress from various sources associates with BMI, waist circumference, and adiposity, potentially linked through elevated cortisol, which influences metabolic function as well as stress response (74–76). For this reason, we examined DNA methylation of *FKBP5*, a gene related to HPA axis functioning. Additionally, the serotonergic system, including methylation of *SLC6A4*, is typically associated with social and emotional reactivity to stress (77), which has direct implications for cardiovascular health (78). Both general trends and specific findings associated with both genes are discussed below.

Embodiment via Epigenetics

In comparing overall findings across methylation analyses, generally we found more significant associations between stressors and resilience factors with DNA methylation among mothers than among children. Though we measured more factors in the mothers, many of the same stressors were significantly associated with methylation in maternal saliva but not in children. In fact, we found mothers had lower levels of DNA methylation in *FKBP5* and higher levels in *SLC6A4* as compared to their children. Decreased methylation at *FKBP5* and increased at *SLC6A4* has been associated with increased stress in this and prior studies. These patterns may suggest that mothers are affected more by the daily stressors they are experiencing than their children, or potentially that mothers have accumulated more epigenetic changes over their life course than children. This result is counter to the hypothesis that childhood is a more sensitive period of development, and may instead support a role for the weathering hypothesis, where effects accumulate over time (26). Alternatively, the mother's own childhood exposures, many prior to migration (which were not measured in this study), may have been more adverse than that experienced by their US-born children.

In comparing across time points, significant epigenetic associations were found at similar frequencies at baseline and follow-up time points. In fact, in many cases the specific findings were similar across time points (with the exception of *SLC6A4* data in the mothers at follow-up, where the sample size was the smallest). The consistency of associations with methylation over time was unsurprising, giving the relative similar reports of stress exposures over time, and the relatively short time period of 2–3 years between samples. This consistency speaks to the relative stability of methylation data over time but also potentially the ongoing challenges faced by immigrant families over the past few decades, and the fact that more recent period of anti-immigrant focused politics in the US may not be a uniquely important stressor experienced in this population.

Despite measuring more stress than resilience factors, we found a surprisingly high number of associations with resilience factors in both mothers and children, justifying further study of epigenetics of resilience. While resilience can sometimes be viewed as simply the inverse of stress (i.e., lack of stress), our findings suggest there may be unique benefits to social support and optimism. These same factors have shown to buffer the effects of adverse childhoods on adult health behaviors and health outcomes (79), and thus the epigenetic effects we detect may be potential mediators along this pathway.

When comparing findings across tested genes, overall *SLC6A4* methylation was associated with more exposure variables than *FKBP5*. Specifically, we found very little significant associations with *FKBP5* in our baseline sample. Only maternal acculturation was associated with lower methylation at this gene, in the expected direction for a stressor in *FKBP5*. Interestingly, we found acculturation was also associated with lower methylation in *SLC6A4,* though higher methylation is expected for stress in this gene. While acculturation can be a stressful process, it can also have health benefits. Our measure of acculturation was a simple measure of language use. More detailed acculturation measures in the future could help clarify what components of acculturation are acting as risk or resilience factors for health, and how they relate to these epigenetic markers.

At the follow-up time point, we found children's reports of everyday discrimination associated with lower methylation at *FKBP5*, and parental social support with higher methylation. These associations were significant even after adjusting for covariates, and were in the expected direction based on prior studies where stress associates with lower methylation at this gene (36, 80). Our findings expand this literature by investigating these associations for the first time in children. The lack of significant findings at this gene in mothers relative to children in our sample may support the hypothesis that there are timing specific effects that may vary by gene, as found in previous longitudinal studies (38).

We found many different stressors associated with increased methylation (i.e., the expected direction) at *SLC6A4* in both children and mothers (e.g., immigrant related stress, fear of parent's deportation) at baseline, while greater subjective social stress was associated with decreased methylation in mothers. To our knowledge, SSS has never been evaluated with epigenetic data before, but appears to be protective against stress-related epigenetic changes in our findings. At follow-up, optimism was associated with lower methylation in children at this gene. In our prior research (53), we found increased optimism to be associated with increased epigenetic age in this same sample of children, which was attributed to potentially beneficial faster child development (e.g., reaching developmental milestones more rapidly). In mothers at follow-up, the few findings (mostly at one CpG site in *SLC6A4*) were inconsistent with baseline trends, and also inconsistent with prior studies. These findings should be interpreted with caution as they could be potentially spurious associations related to the much smaller sample size at follow-up.

In regards to the functional relevance of these results, one noteworthy finding was that methylation at *SLC6A4* was significantly associated with *lower* BMI percentile and waist circumference in the children, but *greater* BMI and higher BP in the mothers, at the follow-up time point. Similar to our findings in the children, one prior study found greater methylation of a CpG site in the same region in *SLC6A4* in blood of adolescents was associated with lower measures of adiposity including BMI, skin fold thickness, and waist circumference (17). Their study also found lower methylation at the same site in obese compared with lean adults in adipose tissue. Another study found no association between methylation at this gene and BMI in adults (81). These findings suggest directions of effect may vary with age, but further study in larger longitudinal samples is needed to clarify these trends.

Given that these same sites of *SLC6A4* also associated with stress factors in our dataset, taken together with these cardiometabolic findings, our data suggest that methylation may be a pathway through which stressful experiences like discrimination can become embodied and ultimately affect cardiometabolic health. Larger and longer-term longitudinal studies will ultimately be needed to formally address the role of this gene in mediating cardiometabolic outcomes across the life course.

Longitudinal Trends

Over time, we found a decrease in mothers' average methylation levels at *FKBP5* and an increase in children's methylation at one CpG site in *SLC6A4*. For *SLC6A4* specifically, we found the effect persisted after adjusting for age, suggesting the increased methylation was not just an aging effect. These longitudinal trends, though small in magnitude, are in the direction expected for increased stress in their environments. In contrast, our measures of stress did not increase over time in mothers, but they did in children, who may have become increasingly aware of adverse sociopolitical environments as they aged. While there have been increasing policies directed against Latinx people during this 2-year study period, these changes may not represent a unique moment in time for this population, who have consistently faced high levels of discrimination and anti-immigrant policies for decades. Thus, this current sociopolitical moment may be less impactful than a lifetime of exposure to these stressors experienced by the mothers, consistent with the weathering hypothesis.

Limitations and Strengths

Several limitations should be noted. First, interpretation of our findings is limited by relatively small sample sizes, especially at the follow up time point. The large attrition was expected, considering how recruitment was limited by several factors regarding the socio-politically stressful time period. This is typical in studies of vulnerable populations as there are inherent difficulties in recruiting a largely undocumented immigrant population (82). The high level of attrition may have biased our sample to retain less vulnerable members of the baseline group, particularly as those who left were more likely to be undocumented and unmarried. This attrition bias could contribute to the lack of a significant increase in stress over the studied time period, despite increasing anti-immigrant policies and rhetoric throughout this period. A second limitation is the lack of generalizability of our findings. While Nashville, TN represents a growing site for immigration settlement, our study is only based in one location in the US South, and the majority of the families were from Mexico, low SES, undocumented. Third, we recognize BMI is not an ideal marker of metabolic risk, as it is biased by design to measure "normal weight" for Western Europeans (83). However, it often has clinical relevance, especially when paired with waist circumference. Fourth, any analysis of DNA methylation in saliva samples cannot be generalized to other tissues of interest. Because saliva samples are made up of both epithelial cells and blood cells, there are concerns of cellular heterogeneity, that are generally difficult to account for with bioinformatic adjustment (84), and is typically only possible in genome-wide studies. Future studies are needed to address this issue, ideally using samples of isolated cell types across tissues. We also note that the methylation detected by bisulfite conversion techniques can't distinguish between 5-hydroxymethylcytosine (5hmC) and 5-methylcytosine (5mC), and thus our methylation estimates represent a mix of both nucleotides (85). Fifth, we only investigated a limited number of sites within two genes; however, these sites were carefully chosen based on prior studies to represent known pathways of stress embodiment. Finally, we recognize that if a Bonferroni correction were applied, few of our associations would pass. However, we note that in an exploratory study of methylation, Bonferroni can be overly conservative, particularly given that methylation levels are correlated across sites, as are the stressors, so they should not all be considered independent tests.

Our study contains a number of unique strengths as well. First, despite a small sample size, our study was unique in the depth of collected data, which includes comprehensive measures of psychosocial stress and resilience. Our survey data were obtained through extensive 2–3-h interviews with the mothers and an hour with the children. Another strength lies in the depth of data from two perspectives—mothers and children. This is especially important as children's perspectives on stress are very underrepresented in the literature, and provide insights on different epigenetic dynamics in different life stages. Further, the longitudinal design permits comparison of stress and methylation across different sociopolitical periods and across a ∼2-year span of childhood. Longitudinal methylation data are very rare, especially during a difficult sociopolitical period for this population. This study is also one of the only studies of stress and methylation in Latinos. Finally, our targeted hypothesis-driven epigenetic approach is valuable, particularly for a focused study with extensive and detailed sociocultural data that are usually very challenging to collect on larger samples necessitated by genome-wide approaches (29).

CONCLUSION

Our findings demonstrate an epigenetic pathway through which early adversity and ongoing stressful life events associate with DNA methylation within important regulatory regions of two well-characterized stress-related genes. This study explored these epigenetic associations within the context of a shifting sociopolitical environment. Many different stressors were associated with both cardiometabolic health markers and DNA methylation in both children and mothers at both genes and across time points. Associations between methylation at *SLC6A4* with cardiometabolic markers implies potential functional relevance of methylation at these sites in contributing to obesity and other cardiovascular or metabolic diseases. Taken all together, our findings suggest that methylation may be a pathway through which stressful experiences like discrimination can become embodied and ultimately affect cardiometabolic health.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Materials**, further inquiries can be directed to the corresponding author.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by Vanderbilt University IRB-Human Research Protections Program; University of California San Diego IRB-Human Research Protections Program. Written informed consent from the participants' legal guardian/next of kin was not required to participate in this study in accordance with the national legislation and the institutional requirements. Oral informed consent was obtained from all participants.

AUTHOR CONTRIBUTIONS

EC and AN conceived of the study. AN coordinated and oversaw all study activities. EC generated the methylation data. All authors contributed to the analysis of the results and wrote the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpsyt.2021.696827/full#supplementary-material

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