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Down and up! Does the mu rhythm index a gating mechanism in the developing motor system?

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ABSTRACT

Developmental research on action processing in the motor cortex relies on a key neural marker – a decrease in 6–12 Hz activity (coined mu suppression). However, recent evidence points towards an increase in mu power, specific for the observation of others' actions. Complementing the findings on mu suppression, this raises the critical question for the functional role of the mu rhythm in the developing motor system. We here discuss a potential solution to this seeming controversy by suggesting a gating function of the mu rhythm: A decrease in mu power may index the facilitation, while an increase may index the inhibition of motor processes, which are critical during action observation. This account may advance our conception of action understanding in early brain development and points towards critical directions for future research.

1. Introduction

Within their first years of life, infants and young children gain an increasing understanding of the actions around them, by recognizing action goals (Woodward and Gerson, 2014), anticipating others' activities (Monroy et al., 2019), and learning from others through imitation (Marshall and Meltzoff, 2014; Hanika and Boyer, 2019). From cognitive neuroscience, we know that the own and others' actions are represented in partially overlapping neural networks in the motor cortex (Bhattacharjee et al., 2021; Iacoboni et al., 1999; Keysers and Perrett, 2004; Li et al., 2020; Rizzolatti and Fogassi, 2014). This has led developmental scientists to apply infant-friendly neuroscience techniques, such as electroencephalography (EEG), to investigate the development of the motor cortex. Specifically, the neural processes in the motor cortex have been associated with a decrease in oscillatory power at 6–9 Hz in infants and 7–12 Hz in young children (the mu rhythm),[3] recorded over central brain regions (Fox et al., 2016; Marshall and Meltzoff, 2011). This decrease in neural activity is often coined *mu suppression* (or *event-related desynchronization*) in the literature and has become a key neural marker for action execution and action observation, specifically in developmental populations (Debnath et al., 2019; Fox et al., 2016; Marshall et al., 2011; Meyer et al., 2020; Monroy et al., 2019; Woodward and Gerson, 2014). For instance, recent studies report mu power decrease during observation of object-directed actions in infants (Chung et al., 2022; Debnath et al., 2019; Karthik et al., 2022; Meyer et al., 2022), toddlers (Antognini and Daum, 2019; Montirosso et al., 2019) and preschoolers (Bryant and Cuevas, 2019; for an overview see Supplementary Table 1). As an example, in the study by Debnath et al. (2019) EEG was measured while 9-month-old infants executed grasping actions (action execution) and observed an experimenter grasp a toy (action observation). Analysis of activity in infants' 6–9 Hz band over central brain regions revealed a decrease in power, both for action execution and observation as opposed to a pre-stimulus baseline. These findings complement a large body of former studies, showing mu power decrease during action observation and execution, reviewed in detail previously (e.g. Fox et al., 2016).

However, recent findings stand in clear contrast with this general notion of the mu rhythm. Two recent studies found a significant increase

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[3] Throughout the paper when referring to differences in mu activity (i.e. mu power increase and decrease) we refer to difference in activity be compared to baseline, unless specified otherwise.

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rather than decrease in mu power during the observation of an action in 10- and 20-month-old infants (Köster et al., 2020) and 4-year-old children (Endedijk et al., 2017). In both studies, this increase in mu power was succinctly localized over the motor regions (see Fig. 1). Critically, Köster et al. (2020) tested the neural activity over the motor cortex in 10- and 20-month-olds and did not only find that the 7–10 Hz activity showed a clear increase during the observation of 12 different transitive actions from video, but also predicted the subsequent imitation performance for this action in 20-month-olds. These studies underline that an increase in mu power during action observation may also play a decisive role in action processing in the developing motor cortex. Can we neglect these findings in light of the abundance of developmental studies reporting mu power decrease or do these findings reflect a real phenomenon?

In our view, several points speak for a real phenomenon: Complementing the evidence from the above-mentioned studies (Endedijk et al., 2017; Köster et al., 2020), an increase in mu power during action observation has likewise been observed in several recent studies (see Table 1). For example, Ruysschaert et al. (2013) reported a significant increase in mu power when 18- to 36-month-olds observed actions presented on a screen. Moreover, a study by Addabbo et al. (2020), originally aimed at investigating the perception of touch, found in an action observation control condition that mu power of 8-month-old infants was significantly increased over centro-parietal areas. Besides this, additional evidence exists at a descriptive level: Marshall et al. (2013) found an increase in mu power in 14-month-olds for observing live manual actions. A study by Upshaw et al. (2016) revealed an increase in mu power for 12-month-olds (with low grip strength), when watching object-directed actions. Finally, de Klerk et al. (2015) recorded the EEG of 7- to 9-month-old infants watching videos of walking actions and their data pointed towards an increase rather than decrease in mu power (as displayed in their Fig. 3b). However, given that the research focus of these studies was directed on the identification of mu power decrease, no statistical tests were conducted for these effects. These studies provide convergent evidence for an increase in mu power during action observation.

Notably, most of the reviewed studies show a high topographic specificity over motor areas (e.g. Endedijk et al., 2017; Köster et al., 2020), which suggests that the increase in mu power during action observation is likely a motor-related process, rather than reflecting a more general (e.g., attentional) phenomenon.[4] Based on this evidence, we propose that a decrease *and* an increase in the mu rhythm play a critical role in the developing motor system. In the following, we suggest how those divergent findings can be integrated within a gating by inhibition theoretical framework and discuss critical implications of this perspective for future neuro-developmental research on action observation, execution and acquisition.

Noteworthy, besides this accumulating evidence for mu power increase, several studies published in the same time period (see Supplementary Table 1), have reported a decrease in mu power during action observation as mentioned above. To date, no single underlying factor has yet been isolated to explain why mu power is increased in some and decreased in other studies. We discuss multiple factors (e.g. spatial blurring of co-occurring activation and inhibition, temporal features, motor experience, task relevance) which likely co-occur and possibly interact in action processing. More importantly, following the introduction of the gating by inhibition account, we will discuss, how this framework may account for both an increase and a decrease in mu power in the motor cortex during action observation. This is based on the view that the increase in mu power reported in several studies should not be neglected in the theory building about the mu rhythm. We conclude with critical directions for future research that would be needed to dissociate those differential findings and effects, in light of this account.

2. Gating by inhibition as an explanatory framework for the mu rhythm in the motor cortex

An influential framework which explains both an increase and a decrease of power in a single frequency band, is the “gating by inhibition” framework, which characterizes the function of the 8–12 Hz alpha rhythm in the adult brain (Jensen and Mazaheri, 2010; Klimesch et al., 2007; Zhigalov and Jensen, 2020). While the alpha rhythm lies in a very similar frequency range as the mu rhythm, its center of gravity is mostly found in parietal and frontal cortical networks. The alpha rhythm has been ascribed the role of a gating mechanism for neural processes: An increase in power of the alpha rhythm indexes the active inhibition of information processing, for example, blocking interfering sensory input during working memory tasks (Jensen et al., 2002). A decrease in power of the alpha rhythm is thought to facilitate attention and mnemonic processes (e.g., Köster et al., 2018; see Köster and Gruber, 2022 for a review). Importantly, in a recent formulation of the gating by inhibition framework it has been highlighted that task-related changes in alpha power may reflect a “redistribution of resources”, with the specific role for inhibiting cortical processes (Van Diepen et al., 2019) and determining which information is passed on to downstream areas (Zhigalov and Jensen, 2020).

Research suggests that the gating by inhibition framework may indeed extend to and explain sensorimotor processes in monkeys (Haegens et al., 2011) and human adults (Brinkman et al., 2014, 2016; Buchholz et al., 2014; Turella et al., 2016). Specifically, in a seminal study, power in the 8–14 Hz rhythm in the motor cortex was decreased when a monkey performed a vibrotactile discrimination task. At the same time sensorimotor processes were reflected in an increase in firing rate of neurons in this area, eliciting activity bursts at much higher frequencies than the mu rhythm (Haegens et al., 2011). Thus, a decrease in mu power may facilitate the innervation of the motor system, which is then reflected in different processes, e.g., the firing of single neurons, which may elicit activity bursts at a higher frequency range. This study provides strong support for the idea of a gating function of the mu rhythm in the motor cortex. It should also be noted that further studies with adults focusing on mu power decrease found inconclusive evidence (Hobson and Bishop, 2016), largely dependent on a chosen baseline, or that even when mu power decrease was reported, it was considerably higher for the performance versus the observation of an action (Hobson and Bishop, 2016; Birch-Hurst et al., 2022).

Does the gating by inhibition framework provide a potential explanatory framework for the mu rhythm recorded over the motor cortex of the developing human brain? This would imply (i) that both an increase and a decrease in mu power could reflect different states (inhibitory/facilitatory) of the same mechanism and (ii) that the mu rhythm may serve a gating function rather than carrying motor information per se (e.g., these may be reflected in higher frequencies; cf. Haegens et al., 2011). From a gating by inhibition perspective, mu power decrease would index a facilitation of motor processes (e.g., when performing an action), while an increase in mu power would index that motor processes are inhibited (e.g., prevent mimicking an observed action). Consistent with this view, many developmental studies reported a decrease in mu power during action execution, while, to the best of our knowledge, no study has documented an increase in mu power during action execution. In addition to the classical perspective on mu power

[4] Given the specific topography in these studies, we also noted that an adult study that has often been referred to in the developmental literature on mu suppression (Muthukumaraswamy et al., 2004) shows a high topographical similarity with the effects reported (Endedijk et al., 2017; Köster et al., 2020; see Fig. 1). That is, besides the overall decrease in mu power reported in their study, there are two noticeable peaks in mu power for the critical contrasts, which are slightly more posterior and lateralized to the C3 and C4 electrodes, which they included in their statistical test (see their Fig. 3; Muthukumaraswamy et al., 2004)

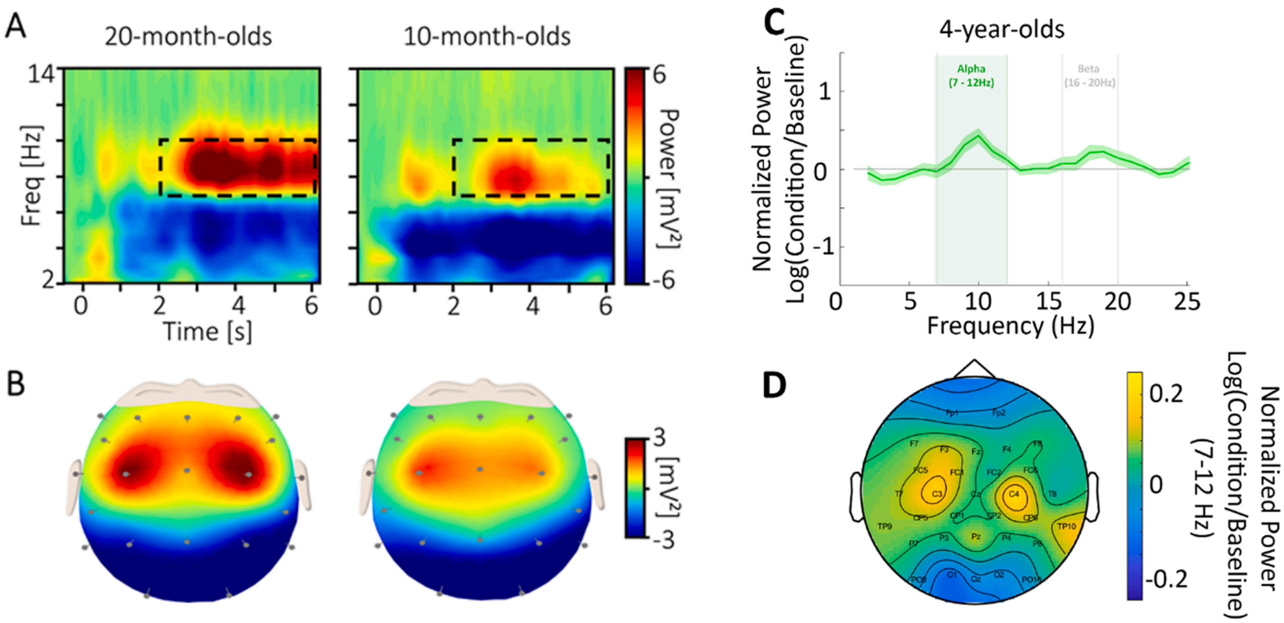

Fig. 1. Two studies reporting mu power increase during action observation. (A) Time-frequency plots show the spectral power at central channels (C3, C4). The dotted rectangle marks infants' 7–10 Hz activity during the presentation of an action (2–6 s), relative to the pre-stimulus baseline. (B) Topographies display the spectral activity for the time-frequency window indicated by the dotted rectangle at C3 and C4, both $p < .001$ (from: Köster et al., 2020; under the creative commons license CC BY-NC-ND 4.0). (C) Normalized power averaged over channels C3 and C4 as a function of frequency shows increase in mu frequency range for 4-year-old children during action observation (top). (D) Topographic distribution of the normalized power in the 7–12 Hz frequency range shows increase in power over motor areas. (from: Meyer et al., 2020; under creative commons license CC by 4.0; see also Endedijk et al., 2017).

decrease, within the gating by inhibition framework, an increase in the mu rhythm may also play a central role in the processing of observed actions, possibly in suppressing the spontaneous imitation of an observed action.

This framework would have critical implications for our understanding and research about neural processes in the developing motor cortex, a developmental period of high plasticity in which observing others' actions and imitating them is pivotal for building up basic motor repertoires. Critically, this framework is not competing with the mirror mechanism but rather broadens the perspective on oscillatory function which may help interpret any mu power changes found over the developing motor cortex. That is, mu power decrease remains a key neural marker for motor system activation in this framework. In the following, we will discuss several developmental studies in light of this perspective and highlight how the gating by inhibition framework may inform our future perspective and research on the mu rhythm in the developing motor system.

3. Developmental findings from a gating by inhibition perspective

Neural mirroring (or common coding) describes the observation that own and others' actions are represented in partially overlapping neural networks in the motor cortex (Bhattacharjee et al., 2021; Iacoboni et al., 1999; Keysers and Perrett, 2004; Li et al., 2020; Rizzolatti and Fogassi, 2014).[5] Critically, such mirroring processes in the motor cortex would also require an effective mechanism to prevent that observed actions are immediately executed, for example during learning novel actions by observation (without direct enactment). From a gating by inhibition perspective, an increase of mu power could serve such an inhibitory function. In fact, in young adults the active inhibition of overt movements has been associated with an increase in mu power (Bönstrup et al., 2015). Similarly, in action observation studies with young children, it is a standard procedure to ask them not to move when observing the action stimuli. This was also the case in the study with 4-year-olds reporting a power increase in the mu rhythm (Endedijk et al., 2017). Although, in contrast to children, infants are not verbally instructed, it is possible that the context of passively viewing videos has a similar inhibitory effect within their own motor system. In support of this notion an EEG study with 18- to 36-month-olds revealed significantly increased mu power for actions presented through video but significantly decreased mu power in response to a live demonstration (Ruysschaert et al., 2013; for similar findings on mu power decrease during live interactions, see Liao et al., 2015; Reid et al., 2011). Evidence remains inconclusive, however, as several recent studies using video stimuli of object-directed actions showed mu suppression in 9-month-old infants (Chung et al., 2022; Karthik, Parise and Liszkowski et al., 2022) and 18- to 24-month-old toddlers (Antognini and Daum, 2019). Therefore, exactly how and which factors elicit a potential inhibitory effect on the developing motor system is unresolved to date. Taking on a gating-by-inhibition perspective on changes in mu power may help in formulating empirically testable hypotheses to resolve this issue. The gating function has also been shown to be critical for social learning (Köster et al., 2020), where an action may be simulated in the posterior motor cortex, but its direct enactment via premotor cortex processes is suppressed. Given the limitations of spatial resolution in the EEG in developmental populations and critical structural differences in the developing motor cortex (Kardan et al., 2022), it is not surprising that an empirical dissociation of different (and potentially co-occurring) inhibitory and facilitatory effects in adjacent brain areas (e.g., in pre- versus post-motor regions) is lacking until to date. In fact, the lack of spatial resolution makes it a tremendous challenge to attribute mu power activity specifically to pre-motor, primary motor or adjacent cortices (an explanation that has previously been proposed for why M1 excitability, as induced by TMS,

[5] Note that this perspective has been complemented in the recent years by findings that critical aspects of others' actions are also processed outside of the motor system (e.g., Tucciarelli et al., 2019; see Thompson et al., 2019 and Wurm and Caramazza, 2021 for recent reviews), a perspective which has not been investigated or discussed in developmental populations and requires further attention in the future.

Table 1
Studies indicating an increase in power of the mu rhythm during action observation in the developing motor system. Unless specified otherwise, the difference in activity is compared to a pre-stimulus baseline and reflects a significant difference from baseline.

Authors	Finding	Age	Frequency	Channel (s)
Addabbo et al. (2020)	Significantly increased power for watching a live simple action (as control condition of a tactile perception study)	8-month-olds	6–8 Hz	Channel cluster around Cp3
de Klerk et al. (2015)	Descriptively increased power for watching videos displaying walking movements (see, pre-training phase).	7- to 9-month-olds	6–9 Hz	Channel cluster around Cz
Endedijk et al. (2017)	Significantly increased power for watching videos displaying object-directed actions.	4-year-olds	7–12 Hz	C3/C4
Köster et al. (2020)	Significantly increased power for watching videos displaying object-directed actions.	10- and 20-month-olds	7–10 Hz	C3/C4
Marshall et al. (2013)	Descriptively increased power for watching live object-directed actions.	14-month-olds	6–9 Hz	C3/C4
Ruysschaert et al. (2013)	Significantly increased power for watching videos displaying object-directed actions; Object observation condition used as baseline	18- to 36-month-olds	Individual peak freq.; mean peak = 8.1 Hz	C3/C4
Upshaw et al. (2016)	Descriptively increased power for infants with low grip strength watching live object-directed actions. Abstract image presentation after observation trials used as baseline	12-month-olds	8 Hz	C4
Van Elk et al. (2008)	Significantly increased power for infants watching walking compared to crawling (i.e., interpreting the findings in terms of walking-crawling, instead of crawling-walking)	14- to 16-month-olds	7–9 Hz	Cz

was not related mu power variations during action observation; Bekkali et al. (2021), Lepage et al. (2008).

Assuming that the mu rhythm serves a gating function, are there specific situations in which motor cortex processes need to be facilitated during action observation, resulting in mu power decrease? This may be the case when the actions performed by others are relevant for the direct and mutual interaction (Meyer et al., 2011; Reid et al., 2011). For example, mu power was decreased when 3-year-old children observed an action while playing a game together with another person, compared to a condition in which the same action was observed outside of a social interaction context (Meyer et al., 2011). This is also in line with recent EEG findings with 9-month-old infants engaged in a turn-taking context (Meyer et al., 2022). Overall, these effects may be indicative for a more fine-tuned interaction between inhibitory and facilitatory processes, which may co-occur in orchestrating action observation, execution, and learning.

This complex interplay between inhibitory and facilitatory processes in conjunction with a lack of spatial acuity in EEG assessments (an issue that is amplified in developmental populations; Kardan et al., 2022) may explain why action observation has also been associated with an increase in mu rhythm activity (see Table 1). In addition, it is well possible that the temporal and oscillatory dynamics of mu power change as a function of age and experience. Especially in the first years of life the brain structure and function undergo drastic developmental changes such as evident in pruning, myelination and changes in functional connectivity (Berchicci et al., 2011; Kardan et al., 2022). To provide two critical considerations in this regard, (i) inhibition of motor processes may be of particular importance in early developmental phases marked by high plasticity of the motor system, and (ii) there is first evidence suggesting an age-related upwards shift in mu peak frequency from infancy to adulthood (Ouyang et al., 2019), which may also be why adult studies often report effects in the adjacent beta rhythm (14–20 Hz).

It has further been shown that visual and motor experience shape action processing as reflected in mu power changes in infants (e.g. Chung et al., 2022; Gerson et al., 2015; Monroy et al., 2019; Paulus et al., 2012). For instance, observing motorically familiar actions elicited a stronger decrease in mu power in 9- and 12-month-old infants than observing novel, tool-use actions (Chung et al., 2022). While likely playing a large role in mu power changes during action processing, motor experience alone is not sufficient to explain the current set of findings (Table 1). That is, for instance in the study by Ruysschaert et al. (2013) the same actions were used in the video-based and live setting. Toddlers showed a significant mu power decrease for observing live actions and a significant mu power increase for observing the same actions on video. Moreover, in the study by Endedijk et al. (2017) 4-year-old children were shown simple goal-directed actions (e.g. pressing a button or shaking a toy rattle) that were well in their motor repertoire and all children successfully reproduced the actions. Therefore, the significant increase in mu power for observing these actions cannot be attributed solely to a lack of motor skill for the observed actions.

When interpreting the up and down of the mu rhythm, it is also important to consider the relative timing and interplay of facilitatory and inhibitory processes. For instance, an increase in mu power following a pre-stimulus baseline may, in principle, result from a decrease in mu power (i.e., facilitatory process) in the sensorimotor system during the baseline. For example, a reduction in mu power in the anticipation of an action has been demonstrated in infants and toddlers who had expectations about an upcoming action (Monroy et al., 2019; Southgate et al., 2009). Besides this, studies with adults have shown that after an action stimulus ends, mu power increases (Babiloni et al., 2002; Schuch et al., 2010, but see Jurkiewicz et al., 2006). These methodological considerations illustrate the complexity of the phenomenon and the need to consider the temporal aspect of mu power changes in developmental populations, and to further resolve processes in pre- and post-motor cortical regions. Taken together, the gating by inhibition account may provide a fruitful framework for interpreting mu rhythm findings in early childhood and may help to further our understanding on how infants' processing of others' actions develops.

4. Future perspectives

Here, we introduce the hypothesis that the mu rhythm serves a gating function in the developing motor system. This theoretical consideration is based on the mechanisms proposed for the alpha rhythm in attention and memory processes in adults (Jensen and Mazaheri, 2010), and recently reported oscillatory processes in the motor cortex in monkeys (Haegens et al., 2011) and adults (Brinkman et al., 2014, 2016).

Despite its appeal, this framework leaves open several questions about the function of the mu rhythm in the developing motor cortex: Can we interpret all former findings in the light of a gating account of the mu rhythm? Are the gating processes in the motor cortex subject to developmental change and how do they relate to the developmental status of early motor capacities? How does mu activity and the gating account relate to early action understanding? How may predictive processes be reflected in motor cortex activity (cf. Köster et al., 2020) and how can they be accounted for in baseline measures (cf. de Klerk & Kampis, 2021; Köster et al., 2021)? Finally, if the mu rhythm serves as a gating mechanism, but does not carry the actual information of an action (whether executed or observed), which are then the functional neural motor and learning processes driving the execution, acquisition and observation of others' actions, in particular in the developing motor system? Future research could adopt the theoretical framework introduced here to empirically dissociate processes, action observation and action execution in particular. Critical methodological considerations include the application of more fine-grained methods to dissociate pre- and post-motor processes, widening the focus to potential interactions with other frequency ranges, the decoding of action-specific information (e.g., Wurm and Lingnau, 2015; for a recent study applying decoding in infants see Xie et al., 2022), and the development of paradigms that specifically dissociate action observation from execution.

To conclude, we are just at the beginning of understanding the neural processes in the developing motor system in action observation, execution, and learning. Applying the gating by inhibition framework to the mu rhythm could be an essential step towards an integration of recent results, which seemed to conflict with the existing literature at first sight, and to guide our future research on the neural mechanisms in the developing motor system.

Declaration of Competing Interest

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

Data Availability

No data was used for the research described in the article.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.dcn.2023.101239.

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