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Motor cortex activity during action observation predicts subsequent action imitation in human infants

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A B S T R A C T

From early on, human infants acquire novel actions through observation and imitation. Yet, the neural mechanisms that underlie infants' action learning are not well understood. Here, we combine the assessment of infants' neural processes during the observation of novel actions on objects (i.e. transitive actions) and their subsequent imitation of those actions. Most importantly, we found that the 7–10 Hz motor cortex activity increased during action observation and predicted action imitation in 20-month-olds ($n = 36$). 10-month-olds ($n = 42$), who did not yet reliably imitate others' actions, showed a highly similar neural activity pattern during action observation. The presence or absence of communicative signals did neither affect infants' neural processing nor their subsequent imitation behavior. These findings provide first evidence for neural processes in the motor cortex that allow infants to acquire transitive actions from others – and pinpoint a key learning mechanism in the developing brain of human infants.

Individuals from many animal taxa rely on social learning (Hoppitt and Laland, 2013). Yet, humans are unique in their ability to use social learning to transmit actions and skills across generations (Boyd et al., 2011; Legare, 2017; Shneidman et al., 2016). Already around their first birthday, human infants begin to imitate others' actions, most notably actions which involve objects (i.e., transitive actions, e.g.; Meltzoff, 1988). It is a basic assumption that infants acquire novel actions from others through neural processes in their own motor cortex (Marshall and Meltzoff, 2015). However, direct evidence for a link between infants' motor cortex activity during the observation of transitive actions and the subsequent imitation of those actions is still missing (Paller and Wagner, 2002).

In adults, own and others' actions are represented in partially overlapping neural networks in the motor cortex (Iacoboni et al., 1999), which suggests a common neural code for own and others' actions (Keysers and Perrett, 2004; Prinz, 1997; Rizzolatti and Craighero, 2004). In infants, the activation of the motor cortex has been associated with a decrease in neural activity in the mu rhythm in central channels in the electroencephalogram (EEG, ~6–9 Hz; Marshall et al., 2011; Saby et al.,

2013; Southgate et al., 2009; van Elk et al., 2008). However, our understanding of the motor system's role in infants' social learning relies mostly on studies of infants' observation of intransitive actions or goal-directed reaching actions, including behavioral experiments (Falck-Ytter et al., 2006; Kanakogi and Itakura, 2011) and EEG studies (Endedijk et al., 2017; Filippi et al., 2016; Hohwy, 2007; Langeloh et al., 2020; Saby et al., 2013). Importantly, when infants imitate others' goal-directed reaching, it is difficult to disambiguate whether infants learnt the performed action in relation to the object or merely encoded the relevance of the target object (Tennie et al., 2009). To pinpoint the neural mechanisms underlying the acquisition of novel transitive actions (i.e., actions performed with an object), it is essential to link the observation of those actions to infants' subsequent imitation behavior (i.e., subsequent memory paradigm; Paller and Wagner, 2002).

Exploring the neural processes that allow infants to acquire novel actions through observation can significantly advance our understanding of early social learning. First, infants' implicit learning and understanding often precedes their explicit behavior (Bergelson and Swingley, 2012; Köster et al., 2019). Therefore, the neuronal dynamics of action learning

may be present already in the first year before infants overtly imitate others' actions.

Second, there is a debate on the role of communicative signals for social learning. Natural pedagogy theory (Csibra and Gergely, 2009) argues that communicative signals facilitate infants' acquisition of novel actions, make those actions more resilient towards counterfactual experiences (Hernik and Csibra, 2015), and induce normative interpretation of novel actions (Király et al., 2013). These effects might be due to qualitative differences in the encoding of communicatively presented information (Yoon et al., 2008, but see Silverstein et al., 2019). If this was indeed the case, we would expect communicative signals to play a critical role in infants' neural processing and the subsequent imitation of transitive actions. However, critics of natural pedagogy theory have argued that differences between communicatively versus non-communicatively presented information can be attributed to differences in attention (Gredebäck et al., 2018). Crucially, the present study allows us to also directly test the effect of the presence or absence of communicative signals on infants' neural processing and imitation learning.

To our knowledge, no study to date has linked infants' brain activity during the observation of novel transitive actions to the subsequent imitation of those actions. Here, we assessed 10- and 20-month-old infants' EEG during the observation of novel actions after a communicative or a non-communicative demonstration, followed by an assessment of 20-month-olds' imitation behavior. This allowed us to examine (1) the neural processes during action observation in 10- and 20-month-olds, (2) whether these processes predict the subsequent imitation behavior in 20-month-olds, and (3) if communicative signals influence infants' neural learning processes and their subsequent imitation behavior.

1. Materials and methods

1.1. Subjects

Forty-two 10-month-old (26 girls, $M = 10$; 23 month; days, $SD = 0$; 11, range; 10; 5–11; 24) and 36 20-month-old (15 girls, $M = 20$; 27, $SD = 0$; 11, range: 20; 13–21; 28), healthy infants, born full term, participated in the study. Participants came from Leipzig, a mid-sized city in Germany. Eighteen additional infants were excluded from the analysis due to fussiness ($n = 9$), technical errors ($n = 3$), or because they refused the EEG cap ($n = 6$). Note that this attrition rate (18.8%) is very low for an infant EEG study. Informed written consent was obtained from one parent before infants took part in the study. The experimental procedures were approved by the local ethics committee.

1.2. Experimental design

In a within-subject design, each infant observed six of 12 actions (see Figure S1) in the communicative (C) condition and six actions in the non-communicative (NC) condition. Each action demonstration trial was presented four times (resulting in 48 trials), divided into four blocks. Several aspects of the design were counterbalanced between subjects: The action presented by the experimenter (see Figure S1), the order of the demonstrated actions, and the demonstration of each action following C or NC signals. Note that we recorded the object presentations by the experimenter (C, NC; first 2 s of the demonstration phase) for each object individually to keep the level of infants' attention high. Given that the experimenter presented the object in full screen (including the face) and the action was shown in a close-up, following a cut, we could perfectly recombine and counterbalance the presentation of the object and the action presentations.

1.3. Stimuli and procedure

The experiment started with a warm-up phase, which was used as a pre-test of infants' basic imitation skills (see basic imitation test in the Methods below). In a live interaction, the experimenter introduced three novel toys and performed two simple actions on each toy. For example, the experimenter showed a toy car and demonstrated that this car could be rolled back and forth and that it had a large button which could be pressed to produce a sound (see Figure S2). Immediately after the demonstration of two actions with each object, the experimenter passed the toy to the infant, allowing the infant to reproduce the actions.

During the EEG session infants sat on their parent's lap at a distance of about 80 cm from a 17-inch CRT stimulus monitor. Sequences were presented full screen. Infants observed 12 actions with different objects on video. The actions in the videos were demonstrated by the same experimenter who also conducted the study. If 10-month-olds were still attentive after the first presentation of all trials, the presentation was started a second time until the infant lost interest. Infants were video-recorded during the EEG assessment for later coding of their gaze behavior.

The duration of the action demonstration videos was 6 s. First, the experimenter was shown, sitting at a table, holding up an object in his left hand (0–2 s). The experimenter either addressed the child and directed the attention to the object (C) or only attended to the object (NC; within-subjects). Specifically, in the C condition the experimenter looked directly at the infant, waved his free hand, and pointed to the object while saying in infant-directed speech "Hey, look over here". In the NC condition, the experimenter looked to the side, then to the object, while making a pointing gesture to his chin and saying in a low pitch voice "Hmm, I'll have look". After the C or NC introduction of the object (0–2 s), the action was repeated 4 times (2–6 s), shown in a close-up (Fig. 1A).

The experimental design also contained a generalization test for a companion study. In this phase, infants watched a brief video (2 s) of an unfamiliar person, performing either the same or a different action with the object from the action demonstration phase. This was to test if infants would generalize the demonstrated action to another individual in the communicative and the non-communicative condition. This phase has not yet been finally analyzed, had a different focus (i.e., a violation of expectation paradigm on infants' generalization learning) and may be published as a companion paper.

Following the EEG assessment, 20-month-olds participated in an imitation test (Fig. 1B). Infants sat on their parent's lap at a table, face-to-face with the experimenter. The experimenter handed the infant each of the 12 objects from the demonstration phase, one after another, for 30 s each. He told the child "Now you can play with it." and asked after approximately 10 s, "How does it work?", and after another 10 s "What does one do with it?" Infants' imitation behavior was video-recorded for later coding.

1.4. EEG recording and analyses

EEG was recorded continuously from 30 Ag/AgCl scalp electrodes, with a REFA amplifier, at 500 Hz, in a shielded room. The horizontal and vertical electrooculogram were recorded bipolar. Cz served as the online reference. Impedances were held below 10 kΩ.

EEG data was preprocessed and analyzed in MATLAB (Version R2017b). EEG signals were band-pass filtered from 1 to 75 Hz and segmented into epochs from -1 – 6.5 s, with regard to the onset of the video. If infants did not watch the full 6 s of the action demonstration, the respective sequence was excluded from the analyses. Furthermore, noisy trials were identified visually and discarded and up to three noisy channels were interpolated ($M = 1.7$, $SD = 1.0$; of the 22 analyzed channels). Eye-blinks and muscle artifacts were detected using an independent component procedure and removed after visual inspection, before further noisy trials were removed, if necessary. Finally, data was re-referenced to the average reference. On average, $M = 36.1$ ($SD = 7.8$) and $M = 33.6$ ($SD = 11.3$) trials remained for the analysis of the action observation phase, for older and younger infants respectively. On average $M = 34.6$ ($SD = 8.8$) trials remained for the observation learning analysis in the 33 older infants, who completed the imitation phase.

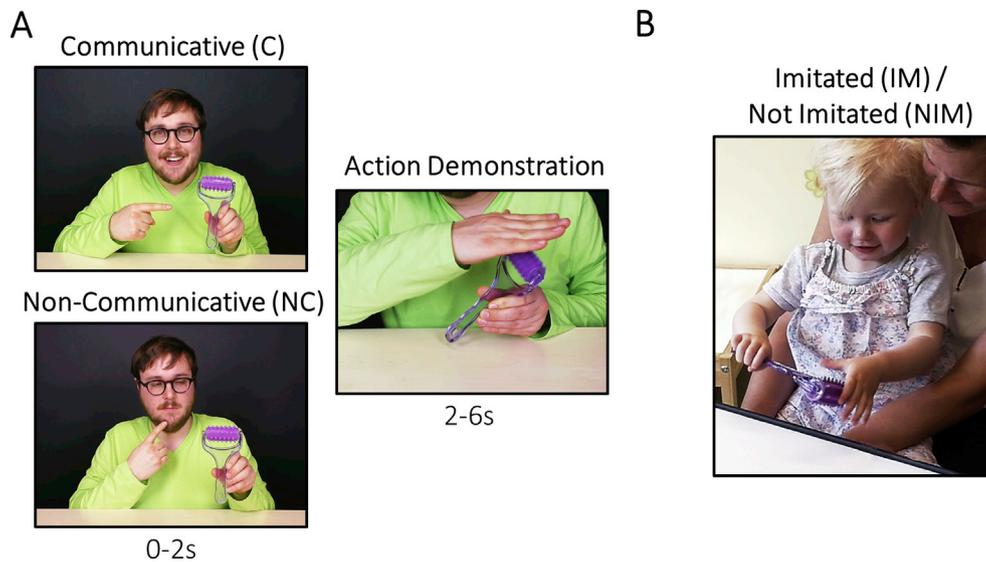To obtain the spectral power over time, the trial data was convoluted

Fig. 1. Sample pictures of the action demonstration and the imitation phase. (A) In each trial of the EEG session, the experimenter presented an object (0–2s), before he performed an action with this object (2–6s), played from video. The action was either demonstrated after a communicative (C) or a non-communicative (NC) presentation of the object. (B) In a subsequent imitation phase, following the EEG session, we tested 20-month-olds' imitation behavior.

using Morlet's wavelets with seven cycles, at a resolution of 0.5 Hz. The spectral power was then averaged over all trials of each condition for the respective analysis. The analyses focused on the electrodes above the hand motor regions, C3 and C4 (Endedijk et al., 2017; Filippi et al., 2016; Langeloh et al., 2020; Saby et al., 2013; for a review, see Marshall and Meltzoff, 2015; for a neuroimaging study in adults, see de Lange et al., 2006). According to previous studies we expected a desynchronization in the 6–9 Hz mu range (Marshall et al., 2011; Saby et al., 2013; Southgate et al., 2009; van Elk et al., 2008). However, the spectral activity at central electrodes revealed a clear decrease in neural activity in the 3–6 Hz range and a clear increase in the 7–10 Hz range, relative to a −0.5 to −0.2 s pre-stimulus baseline. Specifically, we determined these frequency ranges by plotting the neural activity during action observation (2–6 s) at C3 and C4, minus a pre-stimulus baseline (−0.5 to −0.2 s), across both age groups. This revealed a peak decrease (4.5 Hz) and a peak increase (8.5 Hz) in neural activity, ranging from around plus 1.5 Hz to minus 1.5 Hz around this peak (see Figure S3, left panel). This activity pattern was highly consistent across both age groups (see Fig. 2), which was further supported by the results of a cluster permutation test, split by age groups (see Figure S3; cf., Maris and Oostenveld, 2007). In this cluster permutation test, the spectral activity during action observation (2–6 s), at C3 and C4, was tested against a pre-stimulus baseline (−0.5 to −0.2 s) in the 2–14 Hz frequency range (n = 1000 permutations, p-crit = .050, two-sided). The significant negative clusters were 3.0–6.5 Hz (p = .002) for 20-month-olds and 4.0–6.0 Hz (p = .006) for 10-month-olds. The significant positive clusters were 7.5–11.0 Hz (p < .001) for 20-month-olds and 7.0–9.5 Hz (p = .006) for 10-month-olds. Because this is the first study to look at neural activity during the observation of novel transitive actions, we focused the analysis on the most pronounced changes in neural activity during action demonstration. While the 7–10 Hz rhythm was indeed highest at C3 and C4 (i.e., those were the electrodes with the maximum increase in both age groups), the 3–6 Hz desynchronization peaked at posterior electrodes (P3, P4, Pz, P7, P8, O1, O2; i.e., corresponding to the electrodes with a pronounced decrease in both age groups, see Figure S3). The analyses of the neuronal activity during action observation were based on the respective electrode clusters and, conservatively, on the averaged spectral power over the whole time window of the action demonstration (2–6 s) and whole frequency ranges.

The EEG analysis for later imitated (IM) versus not imitated (NIM) actions was conducted with the subsample of infants who completed both the EEG as well as the imitation phase (n = 33; i.e., three infants less than
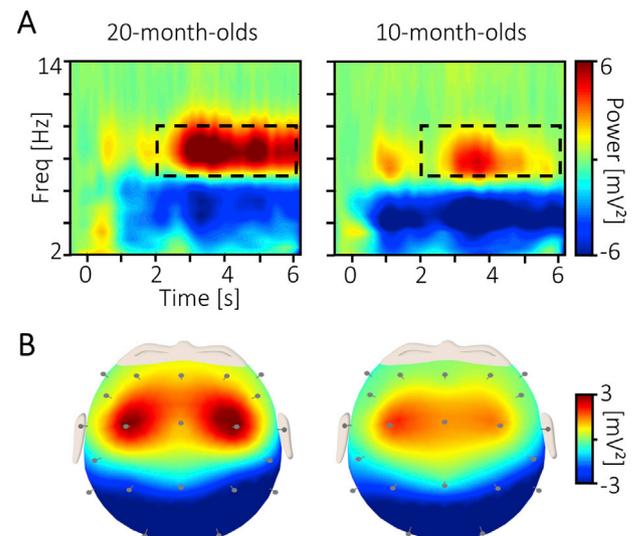

Fig. 2. Infants' brain responses during action observation. (A) Time-frequency plots show the spectral power at central electrodes (C3, C4). The dotted rectangle marks infants' 7–10 Hz activity during action presentation (2–6 s), relative to the pre-stimulus baseline. (B) Topographies display the spectral activity for the time-frequency window indicated by the dotted rectangle. 7–10 Hz activity at C3 and C4 increased in both age groups, both p < .001.

the full sample of 20-month-olds). This analysis focused on the same electrodes (C3, C4) and time-frequency window like the action observation analysis, with regard to a −1 to −0.2 s baseline, prior to the action demonstration. This baseline was used to avoid variances in the EEG signal that arose during the 2 s presentation of the object. We chose a longer time window as a baseline, compared to the initial analysis, because the experimenter's presentation of the object was more variable. Note that communicative signals had no strong effect on 20-month-olds' 7–10 Hz activity (0–2 s), namely this activity was not above baseline (−0.5 to −0.2 s), $t(35)$ = 1.45, p = .156, and did not differ between conditions (C, NC), $t(35)$ = 0.97, p = .336. Furthermore, communicative signals did not affect infants' imitation behavior (see Results). Therefore, the 7–10 Hz activity increased specifically for the action demonstration, and trials with and without communicative signals were equally

distributed between conditions (IM and NIM). Again, the spectral power was averaged across the whole time-frequency range (7–10 Hz, 2–6 s), separated by condition (IM, NIM).

1.5. Imitation behavior

Infants' actions for the 12 objects were coded from video. A coder, who was blind to the actions infants saw during the demonstration phase (i.e., action 1 or action 2 per object), coded both actions per object for each infant. We scored an action as imitated if infants completely reproduced the action or if infants demonstrated a clear attempt to reproduce it (i.e., focusing on how an object was held and moved), to account for low levels of hand motor coordination in 20-month-olds. In case infants showed both actions, we coded the action initiated first, within the 30 s imitation phase. We tested the imitation of all 12 objects. For two infants the imitation of a few objects was not recorded, but nine and six objects remained for the analysis of these two infants, respectively. The interrater agreement established for 13 infants (39.4% of the older sample included in the imitation analysis), was very high $\kappa = 0.94$.

1.6. Basic imitation test

We included a pre-test of infants' basic ability to immediately reproduce simple actions with toys in the warm up phase, which were markedly easier than the actions demonstrated in the EEG session (e.g., moving a toy car back and forth). We coded for each of the three toys if at least one of the two presented actions was imitated. The interrater agreement, established for 20 infants (25.6% of the whole sample), was good $\kappa = 0.88$. While 79.4% of all 20-month-olds reproduced one of the two demonstrated actions for all three toys, this was only the case for 11.9% of the 10-month-olds', $t(74) = 7.98, p < .001$. Because these very simple actions could hardly be imitated by 10-month-olds, subsequent imitation behavior for the actions demonstrated in the EEG session was not assessed in this age group.

1.7. Statistical analyses

We first tested the neural activity during action demonstration (2–6 s) against the pre-stimulus baseline (−0.5 to −0.2) for both frequency ranges (3–6 Hz, 7–10 Hz) at the respective peak electrodes (see Methods), separately for both age groups. Thereafter, we analyzed the 3–6 Hz and the 7–10 Hz activity during action observation with two mixed-model ANOVAs with Age (10 months, 20 months) as a between-subject factor and Condition (C, NC) as a within-subject factor. Please note that we will report the results of the factors Age and Condition in separate parts of the results section (paragraph one and three, respectively) so that the presentation of results follows the same order as our research questions. For the subsequent memory test, we used the baseline corrected neural activity during the action demonstration (baseline: −1 to −0.2 s; see Methods) for both frequency ranges (3–6 Hz, 7–10 Hz) at the respective peak electrodes. We applied a t-test to contrast the activity during the observation of actions that were imitated versus those actions that were not imitated in the subsequent imitation phase.

2. Results

First, we analyzed the neural processes during infants' action observation at C3 and C4, reflecting the neural activity in infants' hand motor regions (e.g., Marshall and Meltzoff, 2015). During the action demonstration (2–6 s), we found an increase in 7–10 Hz activity in 20-month-olds, $t(35) = 5.13, p < .001$, and in 10-month-olds, $t(41) = 3.81, p < .001$ (Fig. 2), in contrast to a pre-stimulus baseline (−0.5 to −0.2 s). The Age * Condition ANOVA for the 7–10 Hz activity at C3 and C4 revealed a main effect of Age, $F(1,76) = 5.48, p = .022, \eta^2 = 0.07$, indexing a lower 7–10 Hz power in 10- compared to 20-month-olds (see Table 1). Furthermore, we found a decrease in 3–6 Hz neural activity. This activity was
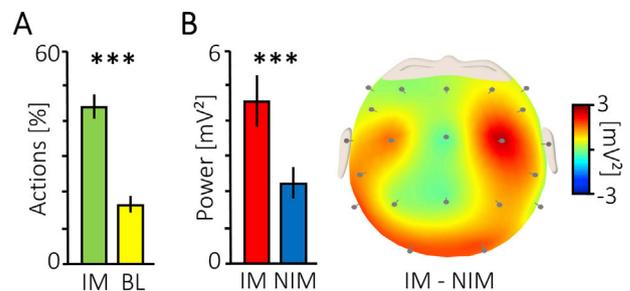

Fig. 3. 20-month-olds' imitation behavior and the neural processes underlying imitation learning. (A) The percentage of actions that were imitated (IM) in the subsequent imitation phase was above baseline level (BL). (B) Bars show the 7–10 Hz response at central electrodes (C3, C4) for the observation of actions (2–6 s) that were later imitated (IM) or not imitated (NIM). The topography shows the corresponding difference (IM – NIM) across all electrodes. ***p < .001.

pronounced at parietal electrodes (P3, P4, Pz, P7, P8, O1, O2) in 20-month-olds, $t(35) = −5.95, p < .001$, and in 10-month-olds, $t(41) = −4.75, p < .001$, (Figure S4). There was no significant difference between groups, main effect Age, $F(1,76) = 1.87, p = .176, \eta^2 = 0.02$. (The main effects for Condition [C, NC] and the interaction effects are reported below.)

Second, we analyzed the neural processes underlying imitation learning in 20-month-olds. The imitation rates for observed actions in 20-month-olds, who completed the imitation phase (subsample of $n = 33$ infants), were $M = 43.9\%$ and clearly above the baseline level $M = 16.5\%$ (i.e., the imitation rate of the second action that infants did not observe), $t(32) = 5.84, p < .001$ (Fig. 3A). Crucially, when we contrasted the neural activity for actions that were imitated (IM) versus not imitated (NIM) in 20-month-olds, we found a higher 7–10 Hz activity for subsequently IM versus NIM actions, $t(32) = 3.55, p < .001$, peaking at C3 and C4 (Fig. 3B). Note that 10-month-olds were not able to reliably imitate much simpler actions in a basic imitation test (see Materials and methods), thus we did not assess their imitation behavior for the actions demonstrated in the EEG session.

Third, we analyzed how communicative signals affected neural processes during action observation and subsequent imitation rates, by contrasting communicative trials (C) and non-communicative trials (NC), within the same ANOVA reported above (see Table 1 for the mean power values and standard errors). Across both age groups, communicative signals had no significant effect on the central 7–10 Hz activity, main effect Condition, $F(1,76) = 1.14, p = .289, \eta^2 = 0.02$, Condition * Age interaction, $F(1,76) = 0.34, p = .564, \eta^2 < 0.01$. There was also no effect on the parietal 3–6 Hz activity, main effect Condition, $F(1,76) = 0.00, p = .999, \eta^2 < 0.01$, Condition * Age interaction, $F(1,76) = 0.39, p = .535, \eta^2 = 0.01$. Likewise, we found no significant difference between the imitation rates for actions presented in the C versus NC condition in 20-month-olds ($M = 46.7\%$ vs. $M = 42.1\%$), $t(32) = 0.72, p = .480$ (see Fig. 3A).

3. Discussion

We found that a higher activity of the 7–10 Hz rhythm in 20-month-olds' hand motor regions during action observation predicted their subsequent imitation of those actions. In light of the common-coding account (Keysers and Perrett, 2004; Prinz, 1997; Rizzolatti and Craighero, 2004), the neural dynamics during action observation may index infants' processing of others' actions in their own motor cortex, allowing them to encode the demonstrated actions and to reenact them later on. Ten-month-olds, who did not yet reliably imitate others' actions, also showed a 7–10 Hz activity over hand motor regions during action observation, but this activity was lower than in 20-month-olds.

The encoding of novel information relies on learning mechanisms,

Table 1
Spectral power during action observation (2–6 s), split by condition.

	Communicative	Non-Communicative
20-month-olds		
7–10 Hz	3.91 (0.77)	3.28 (0.76)
3–6 Hz	−10.21 (2.01)	−9.59 (1.55)
10-month-olds		
7–10 Hz	1.79 (0.52)	1.61 (0.49)
3–6 Hz	−14.71 (3.30)	−15.34 (3.19)

Note: Mean power values (mV^2) and standard errors, at central electrodes (C3, C4) for 7–10 Hz and at posterior electrodes (P3, P4, Pz, P7, P8, O1, O2) for 3–6 Hz.

which are inextricably linked with attentional processes (Cowan, 1988; Tulving and Craik, 2000). This raises the question which specific processes are reflected in the 7–10 Hz activity in the present study. The 7–10 Hz activity was sharply centered over the hand motor regions and increased with the onset of the action demonstration. This suggests that the 7–10 Hz activity may reflect motor cortex processes related to action observation and learning (Marshall and Meltzoff, 2015). In light of the common-coding account (Keysers and Perrett, 2004; Prinz, 1997; Rizzolatti and Craighero, 2004), we assume that these processes index that infants may have simulated others' actions in their motor cortex to encode them.

While the 7–10 Hz activity during action observation was increased above baseline in both age groups in our study, to date many studies have reported a decrease in the infant 6–9 Hz neural activity (Cannon et al., 2014; Filippi et al., 2016; Liao et al., 2015; Marshall et al., 2011; Marshall and Meltzoff, 2014; Saby et al., 2013; Southgate et al., 2009; van Elk et al., 2008). Noteworthy, we showed infants transitive actions (i.e., actions involving an object), while former studies have mainly looked at intransitive actions and goal-directed reaching. In addition, the model in our study repeated the transitive actions several times at a high pace, while most former studies showed a single reach of an object or a single action. These variations in the experimental design could have contributed to the difference in neural activity to previous studies. Importantly, we found that the 7–10 Hz activity increased in both age groups with the onset of the presentation of the transitive action, and that this activity was predictive of older infants' subsequent imitation behavior. These findings suggest that the 7–10 Hz activity is of critical importance for the processing and acquisition of novel transitive actions.

Future research could employ subsequent memory paradigms to ascertain the specificity of the observed effects to infants' acquisition of novel transitive actions as compared to other forms of (motor) learning. Furthermore, we are beginning to better understand the complex interplay of synchronization processes, reflecting inhibition, and desynchronization processes, reflecting a release of inhibition, in the posterior alpha rhythm in adults (Klimesch, 2012). However, it is less clear whether synchronization of central activity in the alpha-band range (i.e., mu) might also be involved in inhibition processes with a functional role in infants' action learning, comparable to a "gating by inhibition" mechanism, as proposed for the adult alpha rhythm (Jensen and Mazaheri, 2010).

Noteworthy, this is one of the first studies which employed a trial-based subsequent memory design to scrutinize learning processes in the infant brain (Paller and Wagner, 2002). While this is a standard paradigm to test neural learning processes in adults (Friese et al., 2013; Köster et al., 2018; for a review, see Paller and Wagner, 2002), subsequent memory paradigms are unfortunately still rarely employed to investigate neural learning processes in the infant brain (Filippi et al., 2016). Our study shows that it is feasible to use subsequent memory paradigms in infants and that they can offer substantial new insights into early learning processes.

The finding that 10-month-olds showed a similar, although lower, 7–10 Hz activity than 20-month-olds supports the idea that neural processes in the motor cortex during the observation of others' transitive actions may already be in place by the end of the first year

(Falck-Ytter et al., 2006; Marshall and Meltzoff, 2015; Southgate et al., 2009). However, at present we can only speculate about the functional role of 10-month-olds' neural processes during action observation. We assume that 10-month-olds already processed parts of the demonstrated actions, but may not yet have been able to imitate others' transitive actions because of their lower motor competencies (cf. Köster et al., 2019). The finding that they failed to imitate even very basic actions during a pre-test supports this interpretation. Critically, in 20-month olds the neural learning processes during the observation of novel actions may be closely linked to their developing motor capacities; they may learn novel transitive actions more easily, when they are similar to their already acquired motor repertoire (Köster et al., 2020). Future studies could further investigate the link between infants' specific motor capacities and their motor cortex activation while observing novel actions.

Despite using a comparatively high-powered design, our study showed no evidence of an effect of communicative signals on infants' learning of transitive actions, neither on the neural processing of those actions in 10- and 20-month-olds nor on the imitation behavior of the 20-month-olds. This suggests that communicative signals may not play a central role in the imitation of transitive actions, particularly in the absence of clear action-related outcomes (cf., no-effect condition in Exp. 2, Kiraly et al., 2013). However, while the within-subject manipulation of communicative signals ensured that children did not show differences in attention towards communicatively and non-communicatively presented information, this may have led to potential carry-over effects between the different communicative conditions. Infants may have perceived the non-communicatively presented trials as communicative, too, because they were presented by the same individual and in the same session (Shneidman et al., 2016). Future studies could investigate potential differences in the effects of communicative signals on infants' retention of transitive and intransitive actions, with a particular focus on the role of communicative signals in linking tools, actions and goals.

Acquiring novel actions from others through observation is integral to human development and the transmission of skills across generations (Marshall and Meltzoff, 2015; Shneidman and Woodward, 2016; Tennie et al., 2009). By combining neural with behavioral measures, we show that 20-month-old infants acquired others' transitive actions via neural processes in their own motor system. Furthermore, we identified similar neural processes in 10-month-olds, who did not yet reliably imitate those actions. These findings shed light on the neural processes by which infants integrate novel actions observed in others in their own motor repertoire – a key mechanism for early social learning.

Declaration of competing interest

There are no conflicts of interest.

CRediT authorship contribution statement

Moritz Köster: Conceptualization, Investigation, Formal analysis, Writing - original draft. **Miriam Langeloh:** Investigation, Writing - review & editing. **Christian Kliesch:** Investigation, Writing - review & editing. **Patricia Kanngiesser:** Conceptualization, Writing - review & editing, Funding acquisition. **Stefanie Hoehl:** Conceptualization, Writing - review & editing, Funding acquisition.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.neuroimage.2020.116958.

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