PAPER





Neural correlates of infant action processing relate to theory of mind in early childhood

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Abstract

The mechanisms that support infant action processing are thought to be involved in the development of later social cognition. While a growing body of research demonstrates longitudinal links between action processing and explicit theory of mind (TOM), it remains unclear why this link emerges in some measures of action encoding and not others. In this paper, we recruit neural measures as a unique lens into which aspects of human infant action processing (i.e., action encoding and action execution; age 7 months) are related to preschool TOM (age 3 years; n = 31). We test whether individual differences in recruiting the sensorimotor system or attention processes during action encoding predict individual differences in TOM. Results indicate that reduced occipital alpha during action encoding predicts TOM at age 3. This finding converges with behavioral work and suggests that attentional processes involved in action encoding may support TOM. We also test whether neural processing during action execution draws on the proto-substrates of effortful control (EC). Results indicate that frontal alpha oscillatory activity during action execution predicted EC at age 3-providing strong novel evidence that infant brain activity is longitudinally linked to EC. Further, we demonstrate that EC mediates the link between the frontal alpha response and TOM. This indirect effect is specific in terms of direction, neural response, and behavior. Together, these findings converge with behavioral research and demonstrate that domain general processes show strong links to early infant action processing and TOM.

KEYWORDS

alpha-ERD, effortful control, mu-ERD, social cognition, theory of mind, theta-ERS

1 | INTRODUCTION

The ability to reason about others' mental states as they relate to behavior (i.e., theory of mind (TOM)), is foundational to social cognitive development and is thought to have roots in infancy (Aschersleben, Hofer, & Jovanovic, 2008; Olineck & Poulin-Dubois, 2007; Sodian, 2011; Sodian et al., 2016; Thoermer, Sodian, Vuori, Perst, & Kristen, 2012; Wellman, Lopez-Duran, LaBounty, & Hamilton, 2008; Wellman, Phillips, Dunphy-Lelii, & LaLonde, 2004; Yamaguchi, Kuhlmeier, Wynn, & vanMarle, 2009). Although there

is some debate about the depth of infants' early understanding of actions (Perner & Ruffman, 2005), infants' behavior is clear: infants systematically respond to others' goal-directed actions (Woodward, Sommerville, Gerson, Henderson, & Buresh, 2009 for review)—often regardless of whether the goal is achieved (Brandone & Wellman, 2009; Carpenter, Akthar, & Tomasello, 1998; Meltzoff, 1995). Before their second birthday, infants also reason about the link between seeing and knowing (Baillargeon, Scott, & He, ; Meltzoff & Brooks, 2008). These abilities are thought to lay the foundation for explicit TOM. Despite considerable interest in the link between infant action

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encoding and later social cognition, the mechanism that supports this link remains largely underspecified. The current study takes a neuroscientific approach to shed new light on the mechanisms that link action processing to TOM.

While there is debate about the factors that support the development of TOM (Ruffman & Perner, 2005), researchers generally agree that processes involved in action perception, planning, and responding to others' actions—referred to broadly as "action processing"—contribute to understanding others' mental states across development (Meltzoff, 1995). In recent years, there have been considerable advancements in the study infant action processing using EEG. Nevertheless, little work has longitudinally examined the association between EEG measures of action processing and later social cognition. The current study has two aims: first, to use neuroscience methods to disentangle the mechanism reported in behavioral studies; and second, to critically evaluate the role that an infant's own actions may play in the development of TOM.

1.1 | Neural measures may disentangle the underlying mechanism

Some of the strongest evidences that TOM develops continuously from infancy to early childhood comes from longitudinal studies that show relations between infants' looking time responses to others' actions and explicit TOM in early childhood (Aschersleben et al., 2008; Sodian et al., 2016; Wellman et al., 2008, 2004; Yamaguchi et al., 2009). Most cases demonstrate a correlation between infant habituation decrement while viewing actions and later TOM. Habituation decrement is thought to index encoding speed and has been linked to several domain general skills (e.g., IQ; Bornstein & Tamis-LeMonda, 1994; McCall & Carriger, 1993). Critically, studies have shown that habituation decrement predicts TOM even when statistically controlling for factors like executive functioning (EF) and language development (Aschersleben et al., 2008; Sodian et al., 2016; Wellman et al., 2008, 2004). Moreover, the link between infant attention and TOM is specific to attention during social events there is no association between infant attention to non-social events and TOM (Yamaguchi et al., 2009). Thus, it has been suggested that the link between infant action encoding and TOM does not reflect individual differences in overall processing speed (or cognitive maturity) but rather reflects individual differences in a cognitive process related to action.

Even so, it remains unclear whether these findings reflect variation in infants' encoding of action structure or instead variation in infants' attention to actions. Neurophysiological data could help to resolve this question. If these behavioral studies do reflect differences in the process of encoding structure in action, as many speculate, we would expect that individual differences in sensorimotor system recruitment may support the development of TOM. The sensorimotor mu-event-related desynchronization (ERD) response is an EEG index of the recruitment of sensorimotor system which has been shown to be involved in encoding of goal-directed actions during action perception tasks (e.g., Cannon

Research Highlights

- These findings are the first to provide neural evidence demonstrating that infant action processing is linked to preschool theory of mind (TOM).
- Seven-month-old infants who showed less occipital alpha-ERD during action encoding show better TOM at age 3.
- Infant frontal alpha-ERD during action production predicted preschool effortful control.
- Infant frontal alpha-ERD indirectly relates to TOM via links to effortful control. This indirect effect is specific in terms of direction, neural response, and behavior.

et al., 2015; Filippi et al., 2016; Southgate, Johnson, Osborne, & Csibra, 2009; Southgate, Johnson, Karoui, & Csibra, 2010). If the connection between infants' action processing and later TOM involves action encoding, then mu-ERD during action observation in infancy would be expected to predict later developments in TOM. Alternatively, the relation between infant habituation decrement and TOM may reflect a domain general skill such as selective/focused attention to action rather than the process of encoding the structure (or goal-directedness) of the action. If this were the case, then we might instead expect that neural indices of attentional engagement (e.g., frontal theta and/or occipital alpha) would relate to TOM. Frontal theta activity has been shown to predict object recognition and attentional engagement in infants (Begus, Gliga, & Southgate, 2016; 2015, & Gliga, 22015; Orekhova, Stroganova, & Posikera, 2001; Orekhova, Stroganova, Posikera, & Elam, 2006) and in adults is linked to attentional and memory processes (Klimesch, 1999; Sauseng et al., 2006). Furthermore, occipital alpha reflects attention to external stimuli and has been shown to respond strongly during infant action perception tasks (Cannon et al., 2015; Filippi et al., 2016; Yoo, Cannon, Thorpe, & Fox, 2016).

Evaluating the neural processes that underlie infant action encoding can dissociate between two cognitive processes (sensorimotor processes and focused/selective attention) that are intertwined in looking time measures. Specifically, the current study examines three neural signatures (i.e., sensorimotor mu-ERD, frontal theta, and occipital alpha) to disentangle the type of processing during infant action encoding that predicts preschool TOM.

1.2 | How could infants' own actions fit in?

To date, studies of infant action processing and TOM focus on action encoding, in part, because encoding other's actions is a plausible foundation for TOM. However, this focus has left an important open question: is action encoding uniquely associated with the development of TOM or could other aspects of action processing (e.g., action execution) also predict TOM? A number of findings suggest that action execution shows important associations with action encoding.

For example, infants' own actions shape action perception (e.g., Ambrosini et al., 2013; Lloyd-Fox, Wu, Richards, Elwell, & Johnson, 2013; Sommerville, Woodward, & Needham, 2005; van Elk, Schie, Hunnius, Vesper, & Bekkering, 2008) and there are associations between sensorimotor mu-ERD during action execution and infant goal encoding behavior (Filippi et al., 2016). Despite several hints in the literature that infants' own actions are meaningfully associated with goal encoding, to date, surprisingly little work has examined the possibility that infants' own actions could be associated with TOM. If infant action perception uniquely predicts TOM, then we would hypothesize that there would not be an association between measures of action execution and TOM. However, if action execution and action perception share a common underlying mechanism, then we might hypothesize that measures of infants' own actions would show similar associations to TOM.

A third alternative also seems possible: it could be that infants' own actions are an index of infants' self-regulation or self-control capabilities early in life. Effortful control (EC) is an aspect of early temperament that reflects one's ability to organize and control goaldirected action and attention. Research suggests that the ability to coordinate goal-directed action develops considerably in infancy (e.g., McCarty, Clifton, & Collard, 1999; von Hofsten, 1991). Several behavioral studies have demonstrated that infant motor behavior can index EF, the cognitive processes that support self-regulation, early in life (for review see: Diamond, 2006), and recent longitudinal (e.g., Libertus, Joh, & Needham, 2016) and correlational studies (Gottwald, Achermann, Marciszko, Lindskog, & Gredeback, 2016) suggest that infants' own actions are associated with broad improvements in attention and EF. Given these associations between infant action and EF (Gottwald et al., 2016; Libertus et al., 2016) and strong associations between EF and TOM (e.g., Austin, Groppe, & Elsner, 2014; Carlson, Mandell, & Williams, 2004), it could be that infants' control of their own actions is a precursor to EC, and that EC in turn predicts TOM. In the current study, we explore both the possibilities that infant action execution is directly associated with TOM, and that neural processing during infant action execution could reflect developmental precursors for EC.

1.3 | The current study

The current study investigates whether variability in neural signatures during action processing (both action encoding and action execution) predict TOM at age 3. To do so, we conducted a longitudinal follow-up of infants who participated in an infant imitation task with simultaneous recording of EEG (originally reported in Filippi et al., 2016). We chose to longitudinally follow the children in the Filippi et al., 2016 study because this EEG study provided rich data about both infants' *neural response* and *behavior* during action execution and during action encoding. In this sample, systematic imitation behavior was directly linked to infants' neural responses during action encoding and action execution. We reasoned that this sample would have sufficient variability in neural response to detect a longitudinal relation to TOM, if such a relation exists. Variability, both

across children and across time, is inherent to developmental change and can be harnessed to understand developmental mechanisms (Siegler & Shipley, 1995). Thus, following this sample allowed us to assess how the neural processes during action encoding and during self-produced action are related to the development of TOM. Our follow-up measures consisted of several validated parent questionnaires indexing temperament, language development, and TOM. We used subscales from each questionnaire to test relations between neural indices, domain general behaviors, and TOM and to evaluate the specificity of these relations.

2 | METHODS

2.1 | Participants

Sixty-three full-term infants participated in an EEG study at 7 months of age. Of these 63 infants, 36 met inclusion criteria for Filippi et al., 2016. When these 36 children reached 3 years of age, their parents were contacted to be a part of a longitudinal follow-up study. The parents of 31 children (15 female children, mean age of children = 37 months 23 days, range = 36 months 11 days-39 months 6 days) consented to participate and completed all the follow-up study surveys.

2.2 | Overview of infant task

At 7-months of age, infants participated in an EEG study investigating the neural correlates of early imitation behavior. Infants were fitted with a 128-sensor Geodesic sensor net (EGI) before engaging in the experimental paradigm. Testing began with a familiarization phase whereby infants engaged one at a time with each of the toys that they would see during the subsequent imitation phase of the experiment. Following familiarization, a curtain came down to hide the stage as an experimenter set up two toys on a small tray. After the toys were set up, the curtain was raised and the infant observed the experimenter grasp one of the two toys. The experimenter then released her grip, looked up, and pushed the tray of toys to the infant. At this point the infant could select between the toys. Infants could either select the same toy as the experimenter (coded as a goal response) or select the previously untouched toy (coded as a non-goal response). Across infants, toy pair was randomized and the side that the experimenter reached to first was counterbalanced, and which toy was the goal was counterbalanced. For further details see Filippi et al., 2016.

Several studies have utilized this paradigm as a means of evaluating whether on average infants have encoded an experimenter's goal (see Gerson & Woodward, 2012; Hamlin et al, 2008; Mahajan & Woodward, 2009). While there are several reasons why the infant may act on the same object as the experimenter (i.e., produce a goal response) during this paradigm, on average (across several studies), infants only systematically act on the goal object when the action is well-formed and they have experience with the action type (see Gerson & Woodward, 2012; Hamlin et al, 2008; Mahajan & Woodward,). Furthermore, research has shown that infants' overt

reproduction of the observed goal (i.e., goal responses) mirrors infant's looking behavior on passive measures of action encoding (e.g., looking time and eye-tracking measures; e.g., Cannon & Woodward, 2012). Thus, we can utilize the proportion of infant's goal responses as an index of their goal encoding.

In the analyses that follow, we distinguish between neural activity when infants observe and then selectively produce a goal response and neural activity when infants observe and subsequently produce a non-goal response. Neural activity preceding a goal response is termed "action encoding" and activity preceding a nongoal response is termed "non-encoding". This terminology clarifies that for each action observation trial we have behavioral evidence of whether or not the infant may have interpreted the goal. We assume action encoding was successful on "action encoding trials" and not successful (based on the infant's failure to reproduce the goal) on "non-encoding trials". 1 While this assumption may not be accurate for every trial (indeed, we cannot know if the infant had other reasons for executing the response that they did), we use this as an approximate indicator based on what we know about infant's average behavioral responses during this paradigm. Further, Filippi et al. (2016) found systematic differences in infants' EEG patterns on goal as compared to non-goal trials.

2.3 | Specific measures-EEG

In the current study, we examine three distinct neural measures during action encoding (i.e., sensorimotor mu-ERD, occipital alpha-ERD, and frontal theta-ERS) and four neural measures during action execution (i.e., sensorimotor mu-ERD, occipital alpha-ERD, frontal alpha-ERD, parietal alpha-ERD). In the sections that follow, we describe each neural signature. We chose to focus on these selected channels and frequency bands to facilitate comparison to prior studies of this sample. In our first report of these data (Filippi et al., 2016), we reported the topography of the effects. Pre-processing was identical to Filippi and colleagues (2016)².

2.3.1 | Action encoding

Action encoding refers to instances when the infant has observed the action event and we have strong evidence that they successfully encoded the event (based on their subsequent behavioral response). In order for any trial to be included: the infant had to remain still during the demonstration phase, attend to the event, and produce a goal response following the demonstration (M = 5, range = 2–9). On average, this subset of the sample attended to the event for 94% of the total duration of the demonstration. To assess specificity, we compare encoding trials to non-encoding trials. Non-encoding trials are identical to encoding trials with one exception—they refer to trials where the infant subsequently produced a non-goal response (M = 5.35, range = 2–10).

Common processing for all action encoding indices

For all neural indices of action encoding (or non-encoding), we computed the average event-related desynchronization (ERD)/

event-related synchronization (ERS) response across all goal response trials for each infant. To do so, we segmented data around our baseline interval (3,000 to 2,000 ms prior to the touch of the toy) which corresponds roughly to the movement of the tray and around our test interval (i.e., the experimenter's touch of the toy; 1,000 ms to 0 ms prior to the touch of the toy). After excluding any trial where the infant produced a movement or did not attend to the stimulus, data from both the baseline and test intervals were Fourier-transformed. ERD/ERS score was computed as 10 times the log ratio of power during the action encoding interval to power during the baseline interval (i.e., decibel difference). The ERD response refers to instances where there is less EEG power in the frequency band of interest during a test event as compared with a baseline period. Thus, more negative ERD values indicate a stronger ERD response. The ERS response refers to instances when there is more power during a test event compared to baseline. Thus, more positive ERS values indicate a stronger ERS response.

Sensorimotor mu-ERD

Prior research has demonstrated that power in the mu-frequency band is reduced over central sites (i.e., corresponding to sensorimotor cortex; Cheyne, 2013) when infants produce actions and when they observe others' actions (Cannon et al., 2015; Marshall, Young, Meltzoff, 2011; Saby, Marshall, & Meltzoff, 2012). Sensorimotor mu-ERD scores were averaged across 6–9 Hz frequency band, encoding trials, and across a group of channels corresponding to C3 and C4 (C3: 93, 103, 104, 105, 111; C4: 29, 30, 36, 41, 42).

Occipital alpha-ERD

To investigate the attentional components of action processing, we also report the occipital alpha-ERD during action encoding. The occipital alpha-ERD response (6–9 Hz) is thought to be an index of visual system engagement and/or attention. To be clear, this directly parallels the sensorimotor mu-ERD with the exception of the spatial location of the clusters used to generate this composite. The occipital alpha-ERD during action encoding was computed by averaging over occipital site clusters surrounding O1 and O2 (O1: 82, 83, 84, 89, 76; O2: 66, 69, 70, 71, 74).

Frontal theta-ERS

To investigate the neural processing involved in focused attention processing, we examine theta-ERS during action encoding. Research suggests that measures of theta amplitude are predictive of focused attention and successful encoding of information both in adults (Klimesch, 1999; Sauseng et al., 2006) and infants (Begus et al., 2016, 2015; Orekhova et al., 2001, 2006). Across both infant and adult studies frontal sites show the strongest effects—as such, in the current study we focus our analyses on frontal scalp sites (however see Data S1 for information on additional scalp sites).

The frontal theta-ERS response was computed using the same methods described above for the sensorimotor mu-ERD and occipital alpha-ERD response with two exceptions. First, to assess *theta* activity, ERS scores were averaged across 4–6 Hz frequency band. Second, we

aimed to assess theta over frontal sites, so we computed band-averaged ERS scores over F3 and F4 (F3: 3, 4, 117, 118, 123, 124; F4: 19, 20, 23, 24, 27, 28)—these site clusters were selected a priori based on the mu-ERD site clusters selected Filippi et al. (2016).

2.3.2 | Action execution

To examine the neural response during action execution, we computed each infant's average alpha-/mu-ERD response across all action execution trials (i.e., during the familiarization phase of the experiment). We chose to examine action execution during the familiarization phase because in this phase the infant executed simple goal-directed actions and their actions were independent of the observation events.

Common processing for all action execution indices

We first segmented data around our baseline interval (3,000 to 2,000 ms prior to the touch of the toy) which corresponds roughly to the movement of the tray and around our test interval (i.e., the infant's touch of the toy; 1,000 to 0 ms prior to the infant's touch of the toy). For focal analyses, data from both the baseline and test intervals were Fourier-transformed and an ERD score was computed as 10 times the log ratio of power during the action encoding interval to power during the baseline interval (i.e., decibel difference). ERD scores were averaged across 6–9 Hz frequency band, all trials, and varied only in the scalp locations. Infants had up to 12 trials of data depending on whether any data were dropped because of artifact, on average 10.19 trials were remaining [range = 5–12].

Sensorimotor Mu-ERD

In the case of the sensorimotor mu-ERD response during action execution, the scalp clusters were identical to the C3 and C4 clusters described above.

Occipital alpha-ERD

The occipital alpha-ERD response was averaged over occipital site clusters O1 and O2.

Frontal alpha-ERD

Frontal alpha-ERD scores were computed by averaging over frontal scalp clusters surrounding F3 and F4 (as described above).

Parietal alpha-ERD

Parietal alpha-ERD to refer to ERD that occurs over parietal scalp sites (P3: 85, 86, 91, 92, 97, 98; and P4: 47, 51, 52, 53, 59, 60).

2.4 | Specific measures-preschooler survey measures

When infants turned 3 years old, parents were sent a series of questionnaires. The surveys included: The Child Behavior Questionnaire (CBQ; Rothbart, Ahadi, Hershey, & Fisher, 2001), the Children's Social Understanding Scale (CSUS; Tahiroglu et al., 2014), Developmental

Vocabulary Assessment for Parents (DVAP; Libertus, Odic, Feigenson, & Halberda, 2015). Parents received a \$20 Amazon gift card in exchange for their completion of all three surveys.

2.4.1 | CSUS

The CSUS provided a measure of TOM which we use as our primary outcome measure. The CSUS asks parents to report on a Likert scale of 1–4 (i.e., definitely untrue to definitely true) what their kids understand about others' behavior and the motivations behind this behavior (See Tahiroglu et al., 2014 for details on psychometric properties of this assessment). The survey's 42 questions comprise six subscales. In the analyses to follow, we averaged all subscales together to create a composite score of TOM understanding. See Data S1 for descriptive statistics for each subscale and histograms of the distribution.

2.4.2 | CBQ

The CBQ is a validated temperament questionnaire that asks parents to report their children's behavior across everyday situations and consists of several subscales involved in temperament and general cognitive development (See Rothbart et al., 2001 for details on psychometric properties of this assessment). The survey's 99 questions comprise 14 subscales. The primary subscale of interest was the EC subscale which is a temperament measure that is thought to capture individual differences in self-regulation and executive attention (Rothbart, Ellis, Rueda, & Posner, 2003). EC has been shown to be related to EF behavior in labbased assessments (Blair & Razza, 2007; Hongwanishkul, Happaney, Lee, & Zelazo, 2005; Johansson, Marciszko, Gredebäck, Nyström, & Bohlin, 2015)-particularly in older children (Johansson et al., 2015; Zhou et al., 2012). While there is debate about the extent to which EC and EF rely on the same underlying mechanisms (Zhou et al., 2012), EC is thought to be particularly relevant for self-regulation of emotion particularly in early infancy. See Data S1 for descriptive statistics for the EC subscale and histograms of the distribution.

2.4.3 | DVAP

The DVAP asks parents to report their children's productive vocabulary from a list of 204 words (See Libertus et al., 2015 for details on psychometric properties of this assessment). Language development has been shown to correlate with TOM (e.g., Astington & Jenkins, 1999; Milligan, Astington, & Dack, 2007). Thus, the DVAP was collected as a control measure with the aim of assessing specificity of observed relations.

2.5 | Analytic strategy

2.5.1 | Preliminary analyses

To begin, we tested whether any of our neural measures showed associations with our preschool questionnaire measures of interest (TOM, EC, productive language) or with each other. See Table 2.

 TABLE 2
 Bivariate correlations between all infant neural indices and TOM at age 3

(13)													1
(12)												1	0.743***
(11)											4	0.655***	0.643***
(10)										1	0.712***	0.543***	***069.0
(6)									T	-0.202	-0.253	-0.095	-0.089
(8)								T	0.257	-0.136	0.101	-0.118	-0.193
(7)							4	0.002	0.072	-0.033	0.134	-0.016	-0.057
(9)						1	0.314+	0.131	-0.108	0.125	0.076	0.007	-0.051
(5)					П	0.068	-0.139	0.018	-0.005	-0.243	-0.074	0.014	-0.059
(4)				1	0.258	0.133	0.047	-0.059	-0.027	0.416*	0.368*	0,466**	0.468**
(3)			\vdash	0.275	0.322	-0.194	-0.165	-0.129	-0.241	-0.027	0.100	0.010	0.020
(2)		1	0.302+	-0.106	0.222	0.233	-0.036	0.009	0.252	-0.404*	-0.472***	-0.193	-0.336+
(1)	1	0.472**	***609.0	960.0	0.435**	-0.120	-0.126	-0.198	0.123	-0.239	-0.040	-0.014	-0.162
	(1) TOM	(2) EC	(3) Productive Language	(4) Sensorimotor mu-ERD	(5) Occipital alpha-ERD	(6) Frontal theta-ERS	(7) Sensorimotor mu-ERD	(8) Occipital alpha-ERD	(9) Frontal theta-ERS	(10) Sensorimotor mu-ERD	(11) Frontal alpha-ERD	(12) Occipital alpha-ERD	(13) Parietal alpha-ERD
	3-year Behavioral	3-year Behavioral Measures		Action Encoding Trials			Non-Encoding Trials			Action Execution Trials			

***p<0.001. **p<0.01. *p<0.05. †p<0.10.

2.5.2 | Focal analyses: action encoding

Preliminary analyses indicated no association between any of our neural measures of interest (i.e., sensorimotor mu-ERD, occipital alpha-ERD, frontal theta-ERS). Thus, to assess the relation between neural correlates of action encoding and TOM, we examined the bivariate correlations between each neural measure and TOM. We applied a Bonferroni correction to correct our three planned contrasts. In those cases that we observed a significant relation between neural correlates of action encoding and TOM, we assessed specificity of the observed relation by testing whether these relations held when controlling for EC and productive vocabulary. In the Data S1 we reproduced these results with regression analysis and simultaneous entry of all neural indices.

2.5.3 | Exploratory analyses: action execution

Next, we tested our exploratory hypotheses about the link between action execution and TOM. Preliminary analyses indicated strong associations between our neural measures of interest (sensorimotor mu-ERD, frontal alpha-ERD, occipital alpha-ERD, parietal alpha-ERD). Consequently, we conducted a regression analysis to assess unique relations between these neural measures and preschool behavior. First, we assessed whether any neural index of action execution predicted TOM. Next, using regression, we examine the possibility that our neural indices of action execution may predict EC. In step 1 of our regression, we control for language so as to identify variance that is unique to EC. In step 2, we enter all action execution neural indices.

In our final exploratory analysis, we use the neural measure that best predicts EC to test whether EC mediates the relation between action-execution processing and TOM. We utilized SPSS's PROCESS macro (Hayes, 2013) to evaluate the mediation effect. This method allows us to use bootstrapping (i.e., resampling 5,000 times), a non-parametric resampling procedure, to estimate indirect and direct effects. Bootstrapping has been shown to have higher power than the traditional Sobel test, while controlling Type I error (Preacher & Hayes, 2004; 2008; Zhao, Lynch, & Chen, 2010). To follow-up on significant effects, we test the specificity of the model in terms of direction, neural index, and behavior with several follow-up models.

3 | RESULTS

3.1 | Preliminary analyses

Preliminary analyses examined descriptive statistics for all neural measures and the relation between all neural indices and TOM and

TABLE 1 Mean neural response for encoding and non-encoding trials

	Action encodi	ng Trials	Non-encoding Trials			
Neural response	Range	Mean (SD)	Range	Mean (SD)		
Sensorimotor mu-ERD	-2.70-1.28	-0.561 (1.06)	-1.98-3.20	0.118 (1.62)		
Occipital alpha-ERD	-4.03-2.49	-0.700 (1.42)	-2.78-1.72	-0.158 (1.16)		
Frontal Theta-ERS	-2.42-4.04	0.558 (1.44)	-2.42-4.04	0.556 (1.44)		

our covariates (EC and productive language) at age 3 (See Tables 1 and 2, respectively).

3.2 | Focal analyses: action encoding

The focal aim of our study was to investigate the link between these components of infant action encoding and TOM. Our original report of this data (Filippi et al., 2016) demonstrated that 7 month olds showed robust mu-ERD over sensorimotor *and* occipital scalp sites on action encoding (i.e., goal response) trials. It could be that the response at both of these sites provides important information about the system involved in infant goal encoding. As such, we first investigated whether either of these neural signatures predicted TOM at age 3. We then examined whether frontal theta-ERS during action encoding predicts TOM. To correct for our three planned contrasts, significance criterion was α < 0.0167 (Bonferroni correction α = 0.05/3).

3.2.1 | Sensorimotor Mu-ERD

Results indicated that the sensorimotor mu-ERD response during action encoding was not associated with TOM (p > 0.606).

3.2.2 | Occipital alpha-ERD

Next, we tested whether occipital alpha-ERD was associated with TOM. Results indicated that the occipital alpha-ERD response did show a significant relation to TOM (r(29) = 0.435, p < 0.014; See Figure 1)-such that a smaller occipital alpha-ERD response (i.e., less recruitment of the visual system) during encoding correlated with better TOM at 3 years. As a follow-up, we tested whether the occipital alpha-ERD correlation was specific by examining occipital alpha-ERD for non-encoding trials. Results indicated that there was no significant correlation between occipital alpha-ERD during non-encoding trials and TOM (p > 0.287). As an additional follow-up, we examined whether the correlation held when controlling for EC and productive language. Results indicated that the correlation remained marginally significant when controlling for EC (r(29) = 0.384, p > 0.036) and became non-significant when controlling for productive language abilities (r(29) = -0.318, p < 0.087). This suggests that the relation between occipital alpha-ERD and TOM may share some variance with language development. See Supplemental Information for further evidence that language may partially mediate the relation between occipital alpha-ERD and TOM and for evidence that the occipital alpha-ERD during action encoding is not associated with orienting and attending to the demonstration.

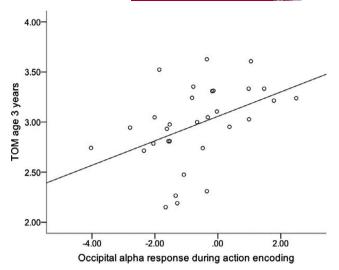


FIGURE 1 Depicts the relation between occipital alpha-ERD during action encoding and TOM at age 3 years

3.2.3 | Frontal theta-ERS

Results indicated that there were no significant correlations between frontal theta-ERS and TOM (ps > 0.384).

3.3 | Exploratory analyses: action execution

In this section, we tested whether any neural measure of self-produced action predicted TOM or EC.

3.3.1 | Neural correlates of action execution and TOM

To evaluate whether neural signatures of action encoding uniquely predicted TOM, we examined whether any neural signatures of action execution could also predict TOM. Results indicated that no

neural index of action execution was associated with preschool TOM (ps > 0.368). Table 2 depicts the bivariate correlations between neural indices of action execution and TOM. There were also no significant associations between any neural index of action execution and TOM after controlling for language (ps > 0.139).

3.3.2 | Neural correlates of action execution predict EC

We next tested whether any neural indices of action execution were associated with EC controlling for productive language. Results demonstrated a robust correlation between EC and frontal alpha-ERD during action execution (β = -0.275, p < 0.025; See Figure 2). This provided evidence that infant action execution predicts EC at age 3. We used this finding as the biological basis for testing an indirect pathway from frontal alpha-ERD to TOM via EC in the next section.

3.3.3 | Mediation: indirect effect-only

We hypothesized that the neural substrates of action execution might be linked to TOM via EC. However, as demonstrated in Table 2 the frontal alpha-ERD response is not directly linked to TOM providing clear evidence that a full-mediation effect does not exist. Nevertheless, several lines of research indicate that the lack of a direct effect does not preclude statistically testing a theoretically motivated indirect effect (for review see: Zhao et al., 2010). Thus, we next evaluated the potential indirect effect proposed (i.e., frontal alpha-ERD \rightarrow EC \rightarrow TOM).

To assess whether EC mediates the relation between frontal alpha-ERD and TOM we conducted a mediation analysis (Model 1: frontal alpha-ERD \rightarrow EC \rightarrow TOM). Results indicated that there was an indirect effect such that infant frontal alpha-ERD predicted EC which in turn predicted TOM (β = -0.0910, 95% level $CI_{bootstrapped}$ = [-0.188-0.038]). However, as was indicated from our bivariate correlations, there was no direct effect (p > 0.213). As

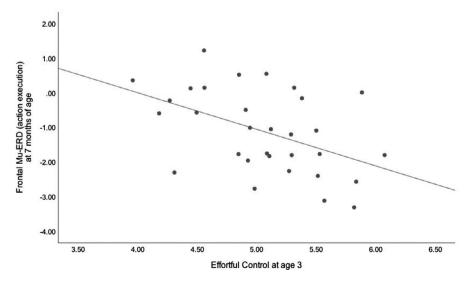


FIGURE 2 Depicts the relation between infant frontal alpha-ERD and effortful control at age 3

Figure 3 demonstrates, infant frontal alpha-ERD during action execution significantly predicted EC (β = -0.211, p < 0.007) and EC significantly predicted TOM at age 3 (β = 0.432, p < 0.004). These results suggest that the mechanism that links action processing to TOM later in life could involve domain general links between the frontal brain processes and EC³.

To test the specificity of this model, we examined whether switching the predictor variable and mediator changed the results. Model 2 examined whether frontal-alpha ERD mediated the link between EC and TOM (Model 2: EC →frontal alpha-ERD →TOM). Results showed a direct effect of EC on TOM (β = 0.432, p < 0.004: $CI_{bootstrapped}$ = [0.153-0.711]) but no indirect effect—suggesting that Model 1's relational pathway may be specific. To further assess the specificity of Model 1, we substituted our vocabulary composite in place of EC in our original model (Model 3: frontal alpha-ERD →productive language →TOM). As we would expect, results indicated that vocabulary predicted TOM (β = 0.008, p < 0.0003) but the indirect effect was not significant-providing evidence that the link between the frontal alpha-ERD response and EC is specific and that EC uniquely mediates the relation between action processing and TOM. To evaluate the specificity of this neural index, we replaced frontal alpha-ERD in our original model with occipital alpha-ERD (Model 4: occipital alpha-ERD →EC →TOM). Results indicated that the model including occipital alpha-ERD showed no significant direct or indirect effects (p > 0.641); there was however, as would be expected a relation between EC and TOM (β = 0.362, p < 0.008)⁴. As a final check of specificity, we evaluated whether this model held when controlling for language (Model 5: frontal alpha-ERD →EC →TOM; controlling for language). Indeed, the indirect effect remained significant when controlling for language (β = -0.0607, 95% level $CI_{bootstrapped}$ = [-0.125-0.0006]). This suggests that the indirect link between frontal alpha-ERD, EC, and TOM is robust and shows considerable specificity.

4 | DISCUSSION

Reasoning about the mental states of others is critical to social development and is thought to derive from early action processing. While a growing number of studies demonstrate that behavioral

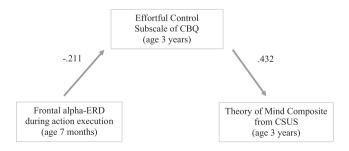


FIGURE 3 Standardized regression coefficients for the relation between frontal alpha-ERD and theory of mind. Mediation model indicates a significant indirect effect

measures of infant visual responses to others' actions relate to TOM in early childhood (Aschersleben et al., 2008; Sodian et al., 2016; Wellman et al., 2008, 2004), these studies leave open the guestion of what neural processes underlie infants' looking behavior. In the current study, we use neuroscience methods to dissociate attentional and sensorimotor components of infant action encoding. Our results demonstrate that attentional processes support the link between action encoding and TOM: Infants that show less occipital alpha-ERD during action encoding show higher TOM scores at age 3. This relation is specific; we do not see the same pattern with sensorimotor mu-ERD, frontal theta-ERS, or with any neural index of action execution. Results also demonstrate that there are strong links between oscillatory brain activity during action execution at 7 months of age and EC 2.5 years later. We demonstrate an indirect link between infant brain activity and TOM that operates via a link to EC. This indirect effect is specific in direction, and in terms of behavior and neural response. These findings are the first to provide evidence that the neural systems associated with both generating motor responses and action encoding are linked to TOM abilities in the preschool years.

Our action encoding results enrich the current TOM literature. While previous studies have hinted that habituation decrement may index encoding of structure in action, our results suggest that the neural processes that support encoding of structure in action, namely the sensorimotor system, are not longitudinally linked to the development of TOM—at least as we've measured them here. Rather, we see a positive association between occipital alpha-ERD and TOM. Occipital alpha is often used as an index of visual attention. In both adults and children, a smaller occipital alpha-ERD response is thought to index less attentional engagement; whereas greater occipital alpha-ERD is linked to greater attentional engagement (e.g., Goldman, Stern, Engel, & Cohen, 2002; Sauseng et al., 2005; Thut, Nietzel, Brandt, & Pascual-Leone, 2006; Xie Mallin & Richards, 2018; Yamagishi et al., 2005). This suggests that those infants who exhibit less attentional engagement (as indexed by a smaller occipital alpha-ERD) when they observe and encode actions show better TOM 2.5 years later. This is not to suggest that infants who show better TOM are looking at the stimulus less. Critically, in order for a trial to be included in our EEG analyses, infants had to watch the entire demonstration. On average, infants looked at the demonstration for 94% of the total demonstration time. Furthermore, our supplemental analyses demonstrate that on action encoding trials there is no association between occipital alpha-ERD and average attention to the demonstration.

While in some ways counterintuitive (i.e., less visual engagement is predicting better outcomes), these results could indicate that those infants who show better TOM do not need to recruit a lot of the brain's attentional resources to encode simple goal-directed actions. The idea that some people recruit less of their brain to perform the same task as others, sometimes referred to as *neural efficiency*, could suggest that children who go on to have better TOM have greater *neural efficiency* in the occipital system. This interpretation is generally consistent with behavioral studies demonstrating that

infants that are faster at disengaging from a repeated action event (e.g., Aschersleben et al., 2008; Wellman et al., 2004, 2008) and that show greater attention flexibility (e.g., Hughes, 1998) exhibit better TOM. However, the idea of differences in neural efficiency in the occipital system requires further empirical support. Alternatively, it could be that there is variability in the time course of the occipital alpha-ERD response which reflects differences in the time course of infant attention. Several eye-tracking studies have demonstrated that infants visually anticipate the outcomes of actions before they are completed and that there are substantial individual differences in action anticipation abilities (e.g., Ambrosini et al., 2013; Cannon & Woodward, 2012). While we were unable to capture fine-grained differences in infant attention, future studies could integrate (and/ or assess the association between) EEG data and several behavioral assessments of action understanding (e.g., looking time, eye-tracking & imitation) to unpack this speculative claim and shed light on our somewhat counterintuitive finding.

Overall, these findings suggest that it cannot be general continuity in cognitive processing that explains our action encoding results. If this were the case, we would expect to see strong correlations between occipital alpha-ERD during encoding and productive language and EC. We do not see any such significant correlations. However, it is interesting to note that when we tested whether our effects held controlling for these two factors (e.g., EC and productive language), the effect held when controlling for EC but not when controlling for language-suggesting that language skills may account for some of the variance linking occipital alpha and TOM (see supplement for further evidence of this claim). These findings could be taken as support for the idea that better visual attention has broad impacts on social cognitive development (Yu & Smith, 2016). Considerable research demonstrates that there are both concurrent and longitudinal links between language and TOM (e.g., Astington & Jenkins, 1999; Milligan et al., 2007). In fact, in our sample, productive language was the strongest predictor of TOM. This could indicate that language development and the domain general skills that support language are foundational to the development of TOM. Alternatively, it could be that the association between language and TOM in our data is artificially inflated because our preschool outcome measures are all parental-report measures and thus exhibit shared method variance. Indeed, to date, researchers are split on the significance of the link between language and TOM (for review see: Milligan et al., 2007). While the current study provides limited evidence on the significance of this link, our data support investigating the link between attentional processes and language development as a means of informing research on the development of fundamental social cognitive skills.

In addition to examining the neural correlates of action encoding, we also examined the neural correlates of action execution. To date, most of the literature on infant action processing and TOM has focused on action encoding because this is a foundational component of TOM, with little attention to possible relations between the processes that support action execution and later TOM. In a series of exploratory analyses, we demonstrate that while no neural measure

of action execution directly predicted TOM, there was an indirect link between frontal alpha-ERD during action execution, EC, and TOM. Broadly speaking, the negative association between frontal alpha-ERD and EC suggests that recruiting the frontal system more during action execution is associated with greater EC later. Indeed, the association between infant frontal alpha-ERD and EC fits with research demonstrating that action production in infancy may involve the development of EF (e.g., Gottwald et al., 2016; Libertus et al., 2016). Unlike our action encoding results, which demonstrated less occipital recruitment during action encoding predicted better outcomes, here we see that greater frontal recruitment is associated with better outcomes. This difference may relate to the type of action processing that infants are engaged in when these neural signals are evaluated (i.e., action encoding for occipital alpha-ERD vs action execution for the frontal alpha-ERD). Variability in the occipital alpha-ERD was not correlated with the frontal alpha-ERD suggesting that these may be unrelated neural signals of distinct domain general processes. It could be that the frontal alpha-ERD response is linked to domain general control processes which are best evaluated when control is being instantiated (e.g., executing an action). Whereas, the occipital alpha-ERD reflects attentional resources recruited specifically during action encoding. The occipital alpha-ERD effect is also specific to encoding trials and is not present on non-encoding trials. Nevertheless, further empirical research, including replication studies, are needed—particularly given the relatively small sample size.

This study provides the first evidence that the infant frontal alpha-ERD response selectively predicts EC at age 3. Critically, this relation is unique-frontal alpha-ERD does not predict productive language and the association between frontal alpha-ERD and EC holds when controlling for productive language. To date, there is limited evidence that the infant neural response is longitudinally predictive of important behavioral markers of cognitive development. This result fits with other work demonstrating that oscillatory activity in frontal brain regions predicts inhibition and cognitive processes in infancy (Bell, 2001; Bell & Fox, 1992). Further, this result demonstrates that variability in the magnitude of the frontal alpha response could be functionally meaningful and tracks with EC. However, further work is needed to understand whether this effect is specific early in development and/ or whether this pattern holds with EF assessments as well. Some research suggests that EF and EC are not associated in infancy at 12 months (Johansson et al., 2015) and may be less similar in younger children than older children (Zhou et al., 2012). This could be due, in part, to the relation between EC and emotional aspects of self-regulation whereas, typically EF assessments are independent of emotion regulation (Posner et al., 2012). Nevertheless, there may be common underlying mechanisms influencing both EC and EF. Thus, further work is needed to replicate these findings and add assessments of EF.

While not a causal link, the relation between frontal alpha-ERD and EC complements several interesting findings that raise the possibility that motor behavior could have cascading effects on domain

general cognitive development—potentially via the pathway of developing control networks in the brain. We show that there is a significant indirect-only mediation (otherwise referred to as an indirect effect) such that the link between frontal alpha-ERD and TOM operates indirectly via EC. This provides a novel mechanistic pathway to TOM that should be further tested with temporally distinct assessments of EC/EF and TOM.

While our research demonstrates links between occipital alpha-ERD and TOM and frontal alpha-ERD, EC and TOM, this is not to suggest that these are the only neural systems associated with TOM. Indeed, several studies (e.g., Bowman, Thorpe, Cannon, & Fox, 2016; Sabbagh, Bowman, Evraire, & Ito, 2009; Redcay et al., 2010) implicate several temporal and parietal regions (e.g., TPJ, STS) as being critical in TOM processing. While EEG does not have the spatial sensitivity to examine these regions, an important direction for future research will be to utilize other imaging modalities to acquire information about activation in other regions known to be involved in attention, motor control, and mature TOM. Indeed, some studies using fNIRS demonstrate that during the observation of action infants as young as 4-6 months show recruitment of the pSTS-TPJ region (Lloyd-Fox et al., 2013). While it still remains unclear whether individual differences in the STS activation are longitudinally predictive of developmental outcomes, using fNIRS to test the relation between areas such as the STS and sensorimotor system could inform our understanding of how systems involved in action perception and action production work together. Future studies might use both fNIRS and EEG to determine whether the strength of the sensorimotor mu-ERD response is related to a network involving both STS and prefrontal regions.

The current findings provide new insights into the developmental processes that support the emergence of TOM, but at the same time the current study had several limitations. First, this study relied on parental report of EC and TOM which could introduce reporter bias. While several studies have shown that parental report measures of EC are correlated with in-lab behavior (Blair & Razza, 2007; Hongwanishkul et al., 2005; Johansson et al., 2015), further followup studies should be done using lab-based assessments for external validation. Additionally, by collecting all outcome measures using parental report we may have also inadvertently artificially inflated associations between preschool measures due to shared method variance. If future studies were to utilize both behavioral assessments and parental report, this could help to address this concern. Second, our measures of EC and TOM were collected concurrently. In order to better understand the causal nature of developments in EC and TOM, future studies should aim to collect these measures several times between age 3 and 5 to facilitate the use of auto-regressive and cross-lagged modeling. Third, while we collected several control measures at the preschool time point, we do not have any early infancy control measures. Without these, we cannot draw strong directional conclusions. Indeed, it is important to note that given the correlational nature of these data we cannot know the exact nature and direction of the associations between neural markers of action encoding/execution and TOM reported. Fourth,

while our exploratory analyses are exciting, our sample size is modest. Further work should aim to replicate these findings with a larger sample both to ensure that the relations hold and to further evaluate whether this study is sufficiently powered to detect longitudinal effects. In summary, while these findings are an exciting first look into the mechanisms that may support TOM, further longitudinal studies are needed.

Together, this work suggests that domain general processes show strong links to early action processing and TOM. These novel findings help to disambiguate the processing that may underlie infant looking time measures. Our results suggest that previous findings may be due to differences in visual attention to actions rather than the encoding of goal structure in others' actions. As a whole, these findings both parallel the behavioral literature and advance our understanding of early neural mechanisms that support social cognition. This work converges with research demonstrating that both attentional processes (Yu & Smith, 2016) and control processes support social cognition. Our exploratory analyses also bring to light novel associations between frontal alpha-ERD during action execution and EC. While future research is needed to understand the significance of these relations, it could be that frontal alpha-ERD is a proto-substrate of later developments in EC. In sum, these findings provide novel evidence about how domain general processing may support TOM development.

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CONFLICT OF INTEREST

The authors listed above have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author (Courtney Filippi, PhD) upon reasonable request.

ENDNOTES

¹ Analyses provided in the Supporting Information describe parallel analyses with all-observation trials (collapsed regardless of infant behavior). These supplemental analyses were not guided by our hypotheses

- but do provide additional detail for comparing our effects to other reports in the literature.
- ² For ease of reference we have reproduced these details in the Supporting Information.
- ³ This significant indirect effect further held controlling for productive language at age 3 (β = -0.0607, 95% level $CI_{bootstrapped}$ = [-0.137-0.011])—frontal alpha-ERD significantly predicted EC (β = -0.226, p < 0.003) and EC significantly predicted TOM (β = -0.268, p < 0.047).
- ⁴ The Supporting Information demonstrated that the same patterns are found if one were to utilize the sensorimotor mu-ERD response rather than the frontal alpha-ERD response.

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SUPPORTING INFORMATION

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