The rhythm of learning: Theta oscillations as an index of active learning in infancy

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ARTICLE INFO

ABSTRACT

Active learning is a critical component of human development, however, the mechanisms supporting it are not fully understood. Given that early learning experiences may affect both infants' immediate learning success, as well as their motivation to learn, it is particularly important to investigate the mechanisms of active learning in this period, when the foundations of learning habits and curiosity are built. Traditional behavioural approaches of studying infant learning face challenges that emerging tools from neuroscience may help relieve. We introduce one such tool, EEG theta oscillations, and propose this neural marker has great potential for offering novel insights into active learning. Theta activity, recorded prior to or during learning, has been shown to be predictive of learning success. We argue that this involvement in memory formation, combined with theta activity's tight association with reward processing, makes theta oscillations a uniquely suited tool for the investigation of motivational mechanisms underlying active learning. We outline research questions as well as methodological approaches pertinent to infant learning and suggest how and why theta oscillations may offer complementary insights. As such, we aim to bridge the gap between cognitive and neural approaches, and advance our knowledge of active learning in development more broadly.

1. Introduction

People learn better when the learning is active and self-directed; however, the reasons for why these benefits occur are only starting to be uncovered. Active learning and its benefits have been a topic of discussion and research across multiple disciplines including educational, cognitive, computational, neural, and machine learning sciences. The factors hypothesised to drive the differences between active and passive learning vary across these disciplines. For example, studies in education have long advocated for improving learner engagement through inquiry-based learning (a learner-led question-focused active learning; Herron, 1971). Cognitive scientists have found that allowing learners to adjust the pace of information flow to their processing speed (Metcalfe, 2002), and adapt the content of learning to their prior knowledge (Markant and Gureckis, 2010), leads to enhanced memory for actively engaged content (Gureckis and Markant, 2012; Markant et al., 2016). In computational psychology and machine learning fields, recent work has explored how active learning may be interpreted under the same mathematical principles as inference from, and demonstration of, taught data, providing a computational level explanation for some of

the success of self-directed learning (Yang et al., 2019). Another aspect of active learning, namely the role of the learner's own motivation to learn, has been explored in recent research studying the neural underpinnings of self-directed and intrinsically-motivated learning (Gruber et al., 2014; Voss et al., 2011). Evidence from these studies suggests that the human brain may be hardwired to experience curiosity and information consumption as rewarding (Gruber et al., 2014; Kang et al., 2009). Moreover, heightened curiosity and active exploration can directly facilitate the neural processes of information encoding and retention (Gruber et al., 2014; Jepma et al., 2012; Kang et al., 2009; Voss et al., 2011). These findings thus offer a plausible mechanistic explanation for the benefits of active learning. Furthermore, some have proposed that allowing individuals to self direct their learning can in turn have a positive effect on the desire to learn, or curiosity, itself (Berlyne, 1966).

However, there is significantly less work examining the process and mechanisms for active learning in early childhood. Given that infants' early learning experiences may influence both their learning success at this critical age, as well as their overall motivation to learn, a scientific focus on these developing processes could have broad implications. It is

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therefore of particular importance to investigate the principles and mechanisms of active learning in early childhood, when the foundations of learning habits and curiosity are built.

Although explanatory models of active learning in childhood are still emerging, much evidence suggests that even infants are indeed active learners. Behavioural studies of infant learning have shown infants allocate their attention to stimuli with optimal levels of predictability (Kidd et al., 2012), tailor their exploration to investigate surprising properties of objects (Stahl and Feigenson, 2015), and selectively seek information from informative social partners (Bazhydai et al., 2020; Begus and Southgate, 2012; Kovács et al., 2014). These behaviours appear geared towards optimising infants' information gain, are consistent with models of intrinsically-motivated, interest-driven learning (Bonawitz et al., 2018; Gottlieb et al., 2013; Lowenstein, 1994), and have been associated with superior learning outcomes (Begus et al., 2014; Lucca and Wilbourn, 2016; Stahl and Feigenson, 2015). While methods such as measuring infants' looking-time, object exploration, or communicative gestures are irreplaceable tools in investigation of infant active learning, behavioural measures alone are subject to interpretation, can fall short of explaining the mechanisms, and cannot offer definitive answers as to what motivates infants' behaviour. For example, an infant shifting their gaze away from a stimulus might indicate they have successfully encoded it (Houston-Price and Nakai, 2004), however longer visual attention can reflect both familiarity as well as unfamiliarity with a stimulus, and does not necessarily predict better learning (Colombo et al., 2001). Similarly, even when responding to infant behaviour leads to better learning (Begus et al., 2014; Goldstein et al., 2010; Lucca and Wilbourn, 2016), what mediates this relationship and what mechanisms support infant learning, can only be speculated.

In line with adult research, and in order to pursue a more direct approach to investigating the mechanisms of active infant learning, we turn to neural markers made available by the relatively recent advent of non-invasive neuroimaging techniques, appropriate for use with wake infants. We review research on one such neural marker, EEG theta oscillations, and hope to demonstrate that this measure can complement the existing behavioural methods, bring us closer to understanding the underlying mechanisms of infant learning, bridge the gap between cognitive and neural approaches to studying active learning in development, and perhaps even help inform broader disciplines such as computational psychology, education, and machine learning.

2. Theta oscillations and learning in the brain

The brain is continuously active, and the spontaneous activity generated by the neurons is organised in a complex system of rhythmic activity. The brain's rhythms determine whether and how external input will be processed, and modulate all mental experience (Buzsáki, 2006). Rhythmic or oscillatory activity in the brain is formed by populations of neurons firing together and being inhibited together, and the speed of oscillations, or the wavelength of the rhythm, determines the temporal windows of processing and the size of neuronal pools activated (Buzsáki, 2006). As such, oscillatory activity enables neuronal populations to work in unison, and multiple brain areas to coordinate activity into large-scale brain networks through phase synchrony (Klimesch et al., 2008). In general, fast oscillators, like gamma rhythm, facilitate local integration, whereas slow oscillators, such as theta activity, connect many neurons in large brain areas, thus facilitating information transfer between different structures of the brain (Buzsáki, 2006).

The relation of different rhythms to cognition has been much studied. One of the first rhythms that has been related to cognitive processes is theta rhythm, defined as the oscillatory activity spanning roughly between 4 and 8 Hz in human adults (Rutishauser et al., 2010), and 3−6 Hz in infants (Orekhova et al., 1999) (note that the frequency ranges differ between the two populations due to developmental changes, but both denote what has functionally been identified as theta oscillations in each population). The cognitive function most extensively related to

theta rhythms, and evidenced both on the level of single cell recordings as well as measured by behavioural performance on various cognitive tasks, is the process of information encoding and memory formation. That is, theta rhythms are associated with learning.

How might theta rhythms be involved in memory formation and learning? Memory formation is thought to result from the modification of synapses and neuronal circuits through long-term potentiation (LTP), a lasting enhancement of synaptic potentials resulting from repetitive stimulation. While LTP has been demonstrated in several brain regions, it is most robust and most documented in studies investigating the hippocampus (Klimesch, 1996). Critically, the induction of this plasticity is favoured by coordinated action-potential timing across populations of neurons (Rutishauser et al., 2010). In particular, in the rodent hippocampus, trains of stimuli delivered at intervals equal to theta frequencies were found to more readily induce LTP than similar stimulation at other frequencies (Greenstein et al., 1988). Thus, inducing theta oscillations during encoding can directly affect the changes in synaptic plasticity; in other words, theta activity can directly modulate memory formation.

In addition to the effects on the single-cell level, animal research has provided numerous studies showing hippocampal theta also affects learning as measured by behavioural performance on various memory tasks. Hippocampal theta activity positively correlated with performance of rodents in a maze task (Olvera-Cortés et al., 2002) and differentiated between correctly and incorrectly remembered odours in a recognition memory task (Wiebe and Staubli, 2001). Critically, like on single-cell level, a causal role for theta activity in learning has also been demonstrated on the behavioural level, using interventions. Administering lesions to the septum (which disrupts the pacemaker for hippocampal theta rhythm), or pharmacologically blocking the cholinergic system (thereby decreasing theta oscillations in the hippocampus), both result in impaired or retarded acquisition rate on classical conditioning paradigms, such as the spatial maze task (reviewed in Nyhus and Curran, 2010; Seager et al., 2002). In contrast, pharmacologically enhancing theta rhythms, by blocking serotonin, resulted in better performance on similar tasks (Stäubli and Xu, 1995). The same effect on learning was achieved when hippocampal theta activity was artificially enhanced by electrical stimulation (e.g. Landfield, 1977). When measuring spontaneous theta activity online and administering training contingent on either episodes of hippocampal theta or hippocampal non-theta states (Seager et al., 2002), theta oscillations during training were found to boost the learning outcome whereas their absence had a detrimental effect. Furthermore, differences in theta activity can differentiate not only successful from unsuccessful encoding within individuals, but the theta activity recorded in the hippocampus prior to conditioning can also predict differences between individual animals in how fast they will learn a new activity (Berry and Thompson, 1978).

In humans, studies investigating the role of theta activity in processes of encoding have relied largely on EEG measurements recorded on the scalp. The relationship between scalp-recorded theta oscillations and encoding success was first demonstrated in a series of studies by Klimesch and colleagues (e.g. Klimesch, 1999, 1996; Klimesch et al., 2008). For example, in a study of 'incidental' learning, the authors found that the items, which were later remembered, were associated with larger theta synchronisation during encoding than items that were not remembered. Similarly, Weiss and Rappelsberger (2000) found that increased oscillatory coherence between frontal and posterior scalp electrode sites, and significant increases in theta power, predicted subsequent recall of items (Weiss and Rappelsberger, 2000). Furthermore, in a study by Guderian et al. (2009), using MEG recordings of theta activity in the medial temporal lobe, demonstrated a strong predictive relationship between theta power, shortly preceding the onset of stimuli, and later recall of that stimuli (Guderian et al., 2009).

Research has also provided evidence on the origin of scalp-recorded theta oscillations in humans, by recording the encoding-predictive theta activity intracranially. Rutishauser et al. (2010) recorded from single

neurons in hippocampus and amygdala while participants were learning new stimuli, and demonstrated that, as in animals, the accuracy of phase-locking of the neurons to the theta rhythm during encoding predicted both whether the stimuli will be remembered or forgotten as well as the subjective strength of the memory (as reported by the participants). Further evidence comes from Fell et al. (2011), who found that the power enhancement of rhinal and hippocampal theta activity, recorded before word presentation, predicted successful encoding in human adults (Fell et al., 2011). Similarly, Lega, Jacobs and Kahana (2012), recording from electrodes implanted in the hippocampus of adult patients, report an increase in power of slow theta to predict successful episodic-memory encoding. Importantly, they also found evidence of phase synchrony between the cortex and hippocampus within the theta frequency band, suggesting cortical-hippocampal communication (Lega et al., 2012).

Although non-conclusive, human research investigating the effect of theta activity on encoding, registered via scalp and intracranial EEG, parallels the well-established findings in animal research, and supports the hypothesis that theta rhythms may induce synaptic plasticity in the human brain. Therefore, the link between cortically recorded theta power and the encoding of new information in humans, demonstrated in studies reviewed above, can be assumed to result from theta activity that is induced into the cortex via cortical-hippocampal feedback loops (Klimesch, 1999; Lega et al., 2012).

3. Theta oscillations, rewards, and active learning

We have suggested that theta oscillations can be used in the investigation of mechanisms of active learning. However, to support this claim, evidence is needed that implicates this rhythm in learning beyond single-cell recordings and incidental learning. As outlined above, aspects considered crucial in active learning are the learners' intrinsic motivation (Gruber and Ranganath, 2019), self-directed attention and control over the information flow (Metcalfe, 2002), and active engagement with the content (Markant et al., 2016). In contrast, the research on the relationship between theta oscillations and learning, reviewed so far, aimed to control for the effects of attentional processes or cognitive effort (Klimesch, 1996). We now turn to the research suggesting (1) that theta oscillations may reflect *active cognitive engagement* during learning, and (2) that this rhythm seems tightly connected to the reward system of the brain, relevant for intrinsically-motivated active learning.

Are theta oscillations associated with cognitive effort or active control of attention? Several studies, in which human adults were tasked with remembering a list of items and were able to predict when items would be presented, an increase in theta activity was observed in *anticipation* of the stimulus presentation. Furthermore, similarly to theta activity during encoding, anticipatory theta rhythms likewise predicted successful encoding (e.g. Fell et al., 2011; Guderian et al., 2009; Rutishauser et al., 2010). This anticipatory activation of theta oscillations led several authors to interpret theta activity as indexing active control of attention and cognitive effort (Bosseler et al., 2013), top-down control for selective encoding of information (Nyhus and Curran, 2010), and intentional activation of a mnemonic context, in which the subsequently presented item can be embedded (Guderian et al., 2009). Thus, observing an increase in theta activity prior to learning itself strongly suggests that theta activity is not only involved in incidental learning, but appears to reflect active cognitive engagement.

In addition to active cognitive engagement, active learning is proposed to be beneficial because it is intrinsically-motivated, that is learning itself is experienced as rewarding. To address whether theta activity could index intrinsically-motivated active learning, we first review studies implicating theta in reward expectancy more broadly. A study recording theta oscillations in rats' orbitofrontal cortex, a part of the brain network coding the expectancy of a rewarding outcome, revealed expectancy of a reward modulated the power of theta activation, predictive of learning success (van Wingerden et al., 2010).

Similarly, when adults were promised high or low monetary rewards for remembering the items on a list of words, a strong predictive relationship was found between the power of prestimulus theta activity over the frontal lobe and subsequent memory performance (Gruber et al., 2013). Importantly, the theta-driven memory enhancement was only observed when learning took place in the prospect of a high reward. The authors conclude that reward anticipation facilitates memory encoding by inducing theta oscillatory activity before an event is perceived, providing a link between theta effects on memory formation and theta in response to reward expectation found in animal research (Gruber et al., 2013). These results converge nicely with a study by Kawasaki and Yamaguchi (2013), who found that frontal scalp-recorded theta activity predicted the capacity of visual working memory and, coupled with frontal beta activity, was affected by the expected reward (Kawasaki and Yamaguchi, 2013). Even more direct evidence for the idea that theta oscillations are modulated by reward expectancy and therefore a promising neural marker for investigation of active learning, comes from a study by Cohen et al. (2012). In this study, scalp EEG over the medial frontal cortex and intracranial EEG from nucleus accumbens were recorded simultaneously, while adult patients took part in a simple reward motivation task (Cohen et al., 2012). The analysis revealed a top-down directed synchrony, whereby (scalp-recorded) frontal theta activity directly influenced the theta activity of nucleus accumbens, and, importantly, this modulation was strongest in anticipation of high rewards. Together, these studies suggest that increased scalp-recorded theta activity, predominantly over the frontal lobe recording sites, is tightly linked to reward anticipation and the subsequent memory formation (Cohen et al., 2012; Gruber et al., 2013).

As opposed to experimental situations, in which clear-cut, immediate rewards can be offered to participants to induce their motivation to encode the presented stimuli, most real-life situations do not offer such a straightforward, external reward for learning. Arguably, it is the individuals' intrinsic motivation to learn, namely their curiosity, that is likely to be the main driver for learning new information in everyday life (Ryan and Deci, 2000). How, then, do theta oscillations relate to intrinsically motivated learning in more ecological or participant-lead situations? In a free, subject-led visual exploration task, Jutras et al. (2013) studied eye-movements and their relation to oscillatory activity in the monkey hippocampus. As monkeys freely explored images, their saccades produced a phase-reset of oscillations in the theta frequency range. This phase-reset, as well as enhanced power of theta oscillations prior to stimulus onset, resulted in superior memory of the visually explored images (Jutras et al., 2013). Similarly, in human adults, theta oscillations, specifically midfrontal theta power, was shown to guide exploration in a dynamic reward-learning task (Cavanagh et al., 2012). These studies demonstrate that, even during a naturalistic task of participant-led exploration, which could be understood as intrinsically motivated sampling of information, theta oscillations are enhanced in primates and humans, possibly serving to establish the optimal conditions for stimulus encoding.

Theta activity has also been shown to be sensitive to stable individual differences in epistemic motivation, defined as the motivation to engage in cognitively demanding tasks (Mussel et al., 2016). The power of theta activity in this study reflected the amount of cognitive resources invested in response to differently demanding tasks; distinguished between individuals' level of epistemic motivation as assessed by a personality test; and predicted participants performance on the tasks (Mussel et al., 2016). Relatedly, states (instead of traits) of epistemic motivation, namely curiosity states, have been shown to enhance learning through increased dopaminergic modulation of activity in the hippocampus (Gruber et al., 2014). These findings show a striking resemblance to studies of theta oscillations and their modulatory effect on learning. Like the neural activation measured in states of curiosity using fMRI (Gruber et al., 2014), theta oscillations, induced by an external or internal reward, were partly localised to the reward circuitry of the brain (e.g. Cohen et al., 2012). Like the curiosity-induced neural

activity identified by Gruber et al. (2014), theta activity was proposed to modulate the effects of the dopaminergic system on hippocampal activity, thereby influencing memory formation (Cohen et al., 2012; Jutras et al., 2013; Orzeł-Gryglewska et al., 2006).

Combined, this evidence strongly supports the idea that theta rhythms can be used as a neural marker in the investigation of active learning. Not only has theta activity, recorded prior or during encoding, been shown to be predictive of learning, theta oscillations appear tightly linked with reward-processing, thereby enabling the investigation of motivational mechanisms underlying active learning.

4. Theta oscillations and infant active learning

The benefits of identifying a neural marker that could elucidate the mechanisms and motivational aspects of learning, without relying on behavioural expressions or self-report, are arguably most obvious when studying nonverbal populations, such as human infants. If theta activity plays a role in infant active learning, as it does in adults, we may expect it to be associated with cognitive processes such as attention, response to error detection, and expectation of information; and crucially, we would expect it to be predictive of learning outcomes.

4.1. Attention

Sustained attention and its neural underpinnings in infants was first systematically investigated by Orekhova and colleagues (Orekhova et al., 1999). In their study, EEG activity was recorded in infants (aged 8–11 months) under three experimental conditions, which the authors defined as: externally-controlled attention; internally-controlled attention; and a baseline condition. They found higher power of theta oscillations (spanning between 3−6 Hz) during internally controlled attention compared to other conditions, predominantly over frontal and temporal recording sites (Orekhova et al., 1999). Importantly, the power of frontal theta activity was shown to correlate with 8-month-olds' ability to maintain internally controlled attention (Orekhova et al., 1999). Although this relationship was not observed in older infants in their study, a recent study has demonstrated a predictive relationship between theta activity and sustained attention also in 12-month-old infants. In a detailed analysis of infants' neural activity and visual attention during free play with objects, theta power preceding each visual fixation was shown to positively predict the duration of that fixation (Wass et al., 2018). Similarly, another recent study defined infant sustained attention (and its termination) by a combination of changes in infant visual orientation and changes in their heart rate. The simultaneous recording of EEG activity and heart rate in 10 and 12-month-olds revealed sustained attention was accompanied by theta activity over the frontal, temporal, and parietal poles, thus cross-validating these different physiological and behavioural indices of attention in infants (Xie et al., 2018). Given that both internally-controlled visual attention and self-guided object exploration could be considered crucial aspects of infant active learning, these findings lend further support to the proposal that theta oscillations may be a good candidate for a neural measure that could elucidate the processes of active learning in infants.

Beyond mere duration of attention, a crucial aspect of active learning is directing attention to the relevant information in the environment. Can theta activity be informative in studying how infants guide their learning according to available information and their prior knowledge? A study by Bosseler et al. (2013), investigating the neural correlates of perceptual narrowing in speech processing, suggests exactly this. They found that before the narrowing of infants' speech perception abilities, 6-month-olds discriminate stimuli (syllables) only based on frequency of presentation, showing increased power of theta activity for frequent syllables, irrespective of language (native/foreign). By 12-months, infants' experience with language leads them to prioritise attending to, and showing greatest theta activity, for information that is most relevant for their language acquisition – syllables of their native language. In

contrast, adults, who are already proficient at their native language, need not invest cognitive effort in processing the already acquired language and therefore show most theta activity during processing of the unknown, foreign syllables (Bosseler et al., 2013). The authors thus concluded that theta oscillations in infants (and adults) reflect the individuals' allocation of attention and investment of cognitive effort in what is most relevant for their learning at different developmental stages.

4.2. Response to error detection (surprise)

Another important aspect of active learning is error detection and subsequent adjustment of learning strategies. Numerous behavioural studies that investigate infants' knowledge and expectations, by exposing them to surprising events, have shown that infants indeed allocate more (visual) attention and direct their exploration towards gaining more information about the unexpected events (e.g. Stahl and Feigenson, 2015; Wynn, 1992). Investigating the neural underpinnings of these learning opportunities that follow unexpected events, Berger et al. (2006) recorded the brain activity of 6−9-month-olds, during presentation of correct and incorrect solutions to simple arithmetic equations. In addition to the previously demonstrated increased looking time after a violation of expectation (e.g. Wynn, 1992), their findings also revealed an increased power of theta oscillations over the frontal central recording site of the infants' brain, following the incorrect compared to the correct solution. In another study, using rhythmic visual brain stimulation, 9-month-old infants observed expected and unexpected outcomes of familiar actions, while visual entrainment was stimulated in theta (4 Hz) and alpha (6 Hz) rhythms (Köster et al., 2019). Results showed a sharp increase in visually entrained theta (but not alpha) activity following unexpected compared to expected outcomes. Both of these studies suggest that theta rhythm,in response to unexpected events, may reflect a learning process, such as updating existing representations or models of the world.

These findings can be related to those of Stahl and Feigenson (2015), in which infants showed superior learning following a violation of expectation, suggested to be mediated by infants' increased interest in the objects behaving in a surprising way (see also Bonawitz et al., 2012). Combined with the increase in theta activity following a violation of expectations regarding arithmetic solutions in the study by Berger et al. (2006) and action outcomes in the study by Köster et al. (2019), this evidence therefore lends further support for theta oscillations reflecting heightened attention or increased interest and cognitive processing, all crucial elements of active learning.

4.3. Expectation of information

While surprising events are by definition unexpected, much of infants' everyday information input is likely to be more predictable. For example, one of infants' most important sources of information is other people, who directly communicate information to infants. Prominent developmental theories suggest infants are sensitive to communicative signals such as direct eye-gaze and infant-directed speech, which are proposed to signal to infants that they are being addressed and lead them to expect transmission of information (Csibra and Gergely, 2009). Indeed, a comparison of infants' neural activity when observing naturalistic social vs. non-stimuli, revealed that 6 and 12-month-olds exhibit more theta activity during social stimuli (Jones et al., 2015), possibly reflecting heightened attention due to the information-rich context that social interactions typically present for infants. Crucially, increased theta activity has not been investigated only *during* social stimulation, where infants may already be learning new information, but also in *anticipation* of information from social partners. In a study in which infants were exposed to adults providing information about novel objects, 11-month-olds exhibited increased theta activity when they could expect to receive information, but before any information was in fact

given (Begus et al., 2016). Moreover, this anticipatory activity was modulated by the informative potential of the adult. That is, infants exhibited higher theta activity in anticipation of a communicative utterance from an informative than from an uninformative adult. These results suggest that infant anticipatory theta activity, like that of adults, may indicate an active preparatory state for learning (Begus et al., 2016), possibly serving to establish the optimal conditions for stimulus encoding on a neural level.

4.4. Learning outcome

As opposed to findings in adult studies, evidence implicating theta oscillations in infant learning is thus far mostly circumstantial and indirect. While the studies reporting infant theta activity, reviewed so far, did not measure infant learning on task, they can be related to other infant and adult studies reporting learning in similar contexts. For example, as mentioned above, violation of expectations, associated with an increase in theta activity (Berger et al., 2006; Köster et al., 2019), has been suggested to result in a state of heightened interest or surprise, and to offer infants a special opportunity to seek and learn new information (Stahl and Feigenson, 2015). Similarly, sustained attention (Orekhova et al., 1999; Wass et al., 2018), selective attention (Begus et al., 2016), exploration of novel objects (Orekhova et al., 2006) and infant directed speech (Orekhova et al., 2006; Zhang et al., 2011), are all situations associated with infant learning. The presence of increased theta rhythms in all these situations may mean that theta activity, shown to facilitate transmission of information between hippocampus and cortical structures and enhancing the effect of long-term potentiation in the hippocampus in adults and animals (Nyhus and Curran, 2010; Seager et al., 2002), is possibly what underlies and facilitates learning in infants as well.

Indeed, a recent study tested and confirmed a predictive relationship between theta activity and learning in infants (Begus et al., 2015). Modulations of frontal theta-band oscillations, recorded with scalp EEG during infants' object exploration, were found to predict infants' encoding of the objects' features, as measured by their subsequent recognition of these objects. Specifically, the larger the difference in power of theta activity recorded during exploration of two objects, the larger the difference in infants' subsequent recognition of these objects. The relationship found was specific to the theta-band oscillations (3−5 Hz) recorded over the frontal cortex and was not present in any other frequency band or scalp area (Begus et al., 2015). The location where the learning-predictive theta modulation was recorded in this study is consistent with adult studies, which showed increased frontal theta power for later recalled compared to later forgotten items in adults (Cavanagh et al., 2012; Sederberg et al., 2003; Weiss and Rappelsberger, 2000). Importantly, the predictive relationship between theta oscillations during exploration and subsequent memory was not mediated by the amount of time infants spent looking at or manually manipulating the objects (Begus et al., 2015). These findings further support the use of theta oscillations in the study of active learning in infancy, having been identified not only as a marker of expectation of information, but also as predictive of *encoding* information.

5. Future directions and limitations for the use of theta oscillations

Thus far, we have argued that measuring theta oscillations can provide a novel method to complement existing behavioural approaches in studying active learning in infancy, and reviewed relevant literature in support of this proposal. In the final section, we first outline a number of lines of inquiry in which theta oscillations could provide useful additional insights; secondly, we propose ways in which different approaches to studying infant active learning could benefit from, and be integrated with, measuring neural oscillations; and lastly, we discuss the limitations of this novel measure.

5.1. Social learning

Several infant behaviours, such as social referencing, babbling, and pointing have been proposed to serve the function of infants actively eliciting and modulating the information they receive from others in social interactions (Bazhydai et al., 2020; Begus and Southgate, 2018, 2012; Goldstein et al., 2010; Stenberg, 2009). While, for example, babbling and pointing have indeed been shown to have an effect on infant knowledge acquisition in various correlational studies (Kimbrough Oller et al., 1999; Stoel-Gammon, 1992), this relationship has been predominantly explained as mediated by a quantitative mechanism, whereby infants' learning is facilitated due to the increased amount of information they receive in response to their behaviours (Hoff, 2003; Petitto, 1988). However, it is plausible that in addition to modulating the amount of information infants receive, responding to infant behaviours may facilitate their learning because these behaviours signal *when* infants are interested or motivated to learn, and *what* they desire to learn about (Begus et al., 2014; Begus and Southgate, 2018). Measuring theta oscillations preceding or during these behaviours may play an important role in revealing which behaviours infants use to solicit information from others. Furthermore, considering that infants' continued production of information-seeking behaviours has been shown to depend on receiving the desired response (e.g., Begus and Southgate, 2012; Kovács et al., 2014), identifying such behaviours and responding to them appropriately might have a dramatic effect not only on infants' immediate learning, but also on the extent to which infants continue to request information.

5.2. Exploration

If free exploration is considered as intrinsically motivated information seeking (Nguyen et al., 2013; Schulz, 2012), the finding that theta activity during free object exploration predicted infants' recognition of object features (Begus et al., 2015), can be related to theories of curiosity-driven or intrinsically motivated learning (Gottlieb et al., 2013; Kidd and Hayden, 2015; Lowenstein, 1994). It can be speculated that infants may have shown more theta activation for objects, which they found more interesting, plausibly because they afforded better learning progress (Gottlieb et al., 2013), or matched an optimal level of discrepancy from infants' current knowledge state (Lowenstein, 1994). Therefore, it could be hypothesised that, in addition to theta activation predicting length of exploration, infants' choices of objects to explore or request information about (for example by social referencing or pointing) could potentially be predicted by measuring theta oscillations. This could have practical applications for development of educational toys as well as other media that infants may interact with, by utilising theta activity to predict what kind of materials may best foster infant learning. Moreover, it may help scientists refine their theories of motivation and exploration, by providing an additional tool to measure physiological individual and trial-by-trial differences and predictors.

5.3. Individual differences

None of the above reviewed studies in infants or adults tested for stable individual differences in theta oscillations and whether this measure could differentiate faster or more efficient learners from ones who are less so. Studies in animals (e.g. Berry and Thompson, 1978) have shown a strong predictive relationship between hippocampal theta, recorded prior to the beginning of a conditioning paradigm, and the speed of subsequent learning, such that rabbits whose most prominent oscillatory activity was in the theta frequency range, learned at a faster rate than those who exhibited higher frequency ranges. While pre-training activity may not be a permanent feature distinguishing individuals, it suggests that a promising line of research may be investigating individual differences in theta activity and their relation to other cognitive functions or environmental factors. The limited research on

this topic in children has so far produced a mixed picture. Higher levels of posterior theta activity has been found in institutionalised children compared to home-raised children (Marshall and Fox, 2004), as well as in children from families with low compared to high socio-economic status (Maguire and Schneider, 2019), both suggesting that higher (baseline or resting-state) theta activity might reflect a maturational lag in the nervous system development. While the latter study also related lower resting-state theta power to better performance on a working memory task (Maguire and Schneider, 2019), it remains unclear how the resting state theta activity compares to theta activity during cognitive tasks, whether the found differences are stable, and whether these measures have any predictive power for learning over development. A recent study partly addressed these questions by relating individual infants' changes in theta activity, over the course of video watching at 6 months of age, to their non-verbal cognitive abilities at 9 months of age (Braithwaite et al., 2019). They found a significant predictive relationship, suggesting that individual differences in frontal theta power increases at 6 months could be used as an early indicator of later cognitive abilities (Braithwaite et al., 2019). Further questions remain as to how stable these individual differences in theta activity (and its relation to cognitive abilities) are and, importantly, whether they can be modulated. Studies in adults have, for example, shown that using audio-visual stimulation to externally enhance theta activity during a retention period can enhance subsequent memory performance (Roberts et al., 2018). Thus, further uncovering the origin, stability, and malleability of individual differences in theta activity could potentially open the doors to research and interventions in cognitive development, directly targeting the neural mechanisms of learning.

5.4. Communication

The use of ostensive cues, communicative cues that signal to a recipient that they are being addressed, has been shown to modulate infants' attention (Farroni et al., 2002), interpretation (Yoon et al., 2008), and subsequent imitation of adults' behaviour (Csibra and Gergely, 2006). Ostensive communication is proposed to lead infants to interpret the communication as conveying (culturally) relevant information (Csibra and Gergely, 2009). It is therefore not surprising that when infants faced two adults ostensively addressing them, significant theta oscillations were found in response to both an informative and an uninformative communicative adult (Begus et al., 2016). Thus, despite discriminating between two informants, infants appeared to have expected information transfer and showed some level of engagement with both adults. An open question that theta oscillations might inform is whether infants would also expect information transfer in third-party communication, whether this would likewise depend on ostensive cues, and whether these expectations are context sensitive (e.g. would the need for information transfer, as in the case of a naïve and a knowledgeable agent, elicit relatively more information expectation than its counterpart).

5.5. Language and entrainment

In addition to the evidence that theta activity, averaged over periods of time, may reflect selective attention to relevant linguistic stimuli (Bosseler et al., 2013), much evidence suggests an important link between the moment-to-moment rhythm of theta oscillations and the rhythm of speech, and how this link may be instrumental in language comprehension. Speech is an inherently rhythmic phenomenon, with the rate of syllable production universally exhibiting a 3- to 8-Hz rhythm, which has been shown to be mirrored by phase-locked theta oscillations in the brain of the listener (Ghitza et al., 2013; Peelle and Davis, 2012). This entrainment, or synchronisation, by which neural oscillations adjust to match the phase of the rhythm of external stimuli, has been suggested to facilitate the parsing of speech into meaningful units, suitable for subsequent decoding, thereby enhancing the

perception and intelligibility of speech (Doelling et al., 2014). Evidence of such entrainment to, or cortical tracking of, continuous speech input was recently found also in 7-month-old infants and was shown to be facilitated when infants listened to infant- as compared to adult-directed speech (Kalashnikova et al., 2018). Investigating the differences in how well infants' neural oscillations track on-going speech can offer new insights into characteristics of speech that facilitate or hinder its intelligibility for infants, might distinguish better and worse language learners, and potentially help inform interventions in case of language delays. Importantly, although entrained theta oscillations are not spontaneous and endogenously generated to the same extent as, for example, theta in anticipation of receiving information, entrained theta activity has likewise been shown to be modulated by the content of the stimuli, beyond the frequencies at which the stimuli was delivered (e.g. in Köster et al., 2019), and can therefore likewise reflect an active process of allocating attention or cognitive resources.

5.6. Attention

Typically, predicting learning success in infants has largely relied on behavioural measures, such as looking time, with the assumption that ceasing to look at a stimulus indicates that infants had successfully encoded the said stimuli (Houston-Price and Nakai, 2004). However, attending to a stimulus for a longer time, does not necessarily predict better encoding or recognition at test (Colombo et al., 2001). Indeed, one infant study demonstrated that the predictive relationship between frontal theta power and learning in infants was not mediated by the length of infants' visual or manual exploration (Begus et al., 2015). These findings suggest that theta activity may be a more sensitive measure of infants' attention or cognitive engagement than behavioural measures alone. Another study reported theta activity to predict the length of infants' subsequent visual attention (Wass et al., 2018), but it only did so when the infants were playing with objects on their own, and not when their (visual) attention was guided by an adult partner. Thus, measuring theta activity can offer us insights into infants' intrinsically-guided attention beyond its behavioural manifestations, as well as enable us to study how infants' attention is affected by external factors such as social interactions.

5.7. Causal reasoning

Another area where measuring theta oscillations may be able to provide a unique insight into infants' active learning is causal reasoning. Identifying a cause of any phenomenon, by distinguishing spurious correlations from unconfounded evidence, is a challenge in everyday reasoning as well as fundamental to learning. Children have been shown to distinguish genuine causes from spurious correlations (e.g. Gopnik et al., 2001) and, when given ambiguous evidence, pre-schoolers spontaneously select and design informative interventions to reveal the causal relationships between the objects they are engaged with (Cook et al., 2011). While several studies have shown that children are sensitive to whether the evidence they observe is confounded (e.g. Schulz and Bonawitz, 2007), that they can integrate disambiguating evidence across trials (Bonawitz et al., 2019), and that they can even actively seek and generate their own disambiguating information (Lapidow and Walker, 2019), less is known about these processes in infants. Before the age of 2 years, infants have limited means of acting on the world themselves and much of their causal learning depends on observing others' interventions and drawing the correct inferences. Whether or not infants distinguish confounded from unconfounded data about a causal structure is a research question that could be informed by measuring theta oscillations. If infants distinguish situations in which they will receive disambiguating information from those in which information remains confounded, an increase in theta oscillations would be expected in anticipation of disambiguating information. Furthermore, the extent to which infants exhibit selective theta activity, in

scenarios where they can expect disambiguating information, might also predict whether or not infants will successfully learn new causal structures. Thus, measuring theta oscillations, as a marker of information expectation, might provide new insights into the learning mechanisms of, and individual differences in, early causal reasoning.

5.8. Integrating theta oscillations with other approaches studying infant learning

As already outlined above, theta oscillations can complement and enrich the insights we can gain from studying infant behaviour. For example, measures of visual attention can be predicted by preceding neural activity (Wass et al., 2018), and in some cases better predict the learning outcomes than visual attention alone (Begus et al., 2015). In other cases, measuring neural underpinnings of behaviour can also distinguish between different interpretations of the same behaviour. By demonstrating, for example, that certain contexts or characteristics of social partners elicit an expectation of information, as indexed by increased theta oscillations, the motivation that drives differences in infants' behaviour toward these different social partners can be re-interpreted. Reconsidering infant behaviour in light of the underlying neural activation can thus directly advance our theories on cognitive development. Moreover, neural measures provide rich data that enable analyses going beyond mere group comparisons or investigating differences between experimental conditions. As already exemplified in existing infant studies measuring theta oscillations, this approach allows: examining moment-by-moment changes in infant cognitive processing (Wass et al., 2018); externally enhancing oscillatory activity (Köster et al., 2019) and thereby potentially manipulating the processing itself; and exploring individual differences in neural activity and how they relate to developing cognitive abilities (Braithwaite et al., 2019).

Although collecting EEG data from infants can be challenging (see limitations section), theta oscillations can be approached through various experimental designs, offering a flexible range of measurements. For example, while time-frequency analysis allows for investigation of activity unfolding over time and is suitable for studying time-locked stimulus processing, frequency analysis ignores the time component and could therefore be used in less time-constraint experimental designs, such active learning during free play (as in Begus et al., 2015). A combination of frequency analysis (e.g. in a free play learning session) and time-frequency analysis (during a test when a learning outcome is assessed) could allow for greater freedom and construction of innovative paradigms that are more ecologically valid and suitable for studying active learning. On a finer scale, precise time-locking of measures such as eye-movements and the co-occurring neural oscillations can provide previously unavailable insights into learning. It has been proposed that the timings of eye-movements during visual exploration and theta oscillations synchronise in order to coordinate neuronal activity with the incoming sensory input (Jutras et al., 2013), much like the theta entrainment to speech stimuli. Such synchrony can be thought of as encoding a neural expectation about when critical information is likely to arrive (Peelle and Davis, 2012), is believed to provide optimal conditions for stimulus encoding, and may be important for gating information flow and guiding memory formation (Siapas et al., 2005). Thus, concurrently recording, for example, infant eye-movements and theta oscillations, using time-synchronised eye-tracking and EEG recordings, could lead to a richer understanding of the mechanisms and cognitive neuroscience of infant learning.

Indeed, measuring theta oscillations during active learning tasks may also provide critical data to inform computational theories of attention, surprise, exploration, and learning in early development. Computational models are often used as a tool to improve the transparency and predictive specificity of psychological theories. These models have great potential explanatory power, but are often limited by the richness of the to-be-explained data set. A common challenge for modelling developmental data lies with impoverished datasets. Infants are a costly population to recruit for studies, can only sit through a limited number of trials, and behavioural assays are often limited to a few responses (such as measuring a single grasp or the length of a single look). This leads to a lack of quantitative data that would be necessary for distinguishing between models that produce otherwise qualitatively similar predictions.

Theta oscillations provide a rich, and continuous measure of information that can help inform quantitative differences in computational models of psychology that similarly depend on continuous, probabilistic content. Some computational models predict the degree to which a system responds following evidence, such as models of surprise, which measure the degree to which information is unlikely given a currently held belief or prediction (Shannon, 1948). These models could be linked with both theta activity and other physiological measures (like pupillary dilation) to provide more precise tests of a model's predictive accuracy of surprisal. Surprisal can also be linked to learning, such as KL divergence or Bayesian surprise models that measure the degree to which the probability of the distribution of beliefs shifts after observing data (Kullback, 1968). If theta activation also captures the system "gearing up" to learn new information following a sudden shift in information, this can provide another means to assess models that predict the measure of shifting beliefs following evidence.

Other models provide rational accounts of how an "optimal" agent should behave to gather information, and treat information as a type of reward. For example, models that employ Information Gain provide a mechanism to capture decision making in active learning, by producing predictions about the degree to which particular interventions will be informative for discerning between competing hypotheses, following KL divergence (e.g. Nelson, 2008, 2005). If our proposal that theta activation measures expectation of information is correct, then such measures can tell us whether infants are sensitive to differences in informativeness. Furthermore, coupling theta measures with eye-tracking or preferential looking measures allows us to compare these behavioural responses to predictions of optimal decision making in active learning tasks, and thus informs our understanding of early developing learning mechanisms.

Finally, theta oscillations not only provide a continuous metric with which to evaluate probabilistic models of cognition, but it may also play an important role in how we think about building models of learning under physically constrained, resource rational systems (Lieder and Griffiths, 2020). Bayesian models of belief updating provide theoretically compelling principles of learning, but there is a growing demand for models that integrate these principles of learning with affective states (e.g. Bonawitz, 2018; Li et al., 2019; Persaud et al., 2020). Such integration requires information about the physiological components that might constrain or moderate learning. To illustrate, the degree to which an otherwise "Bayesian learner" updates their individual beliefs given the likelihood of the observed evidence and their prior beliefs, may also be moderated by the degree of physiological response that is produced. For example, inducing physiological surprise may lead to increased learning (Brod et al., 2018). Measuring this affective response may thus inform resource rational models. Physiological responses like theta activity can temporarily stand-in for the latent variables that lead to these differently-effective affective states and influence learning. Measuring theta oscillations could thus help us predict when to expect differential learning across individuals, or differences within the same individual at different times, despite matched evidence and prior beliefs. Theta activation may therefore not only inform our models of children's learning, but also provide an additional component that describes and predicts individual differences in learning operating over otherwise rational models. Combining the power of theta activity's continuous data with probabilistic models of cognitive development provides a unique opportunity to test, refine, and expand our psychological theories of attention, surprise, decision making, and learning.

5.9. Limitations of measuring theta oscillations

While much research suggests theta oscillations are associated with various aspects of active learning, it is important to emphasise that all neural correlates, including theta oscillations, are informative and interpretable only when the experimental paradigm itself provides a strong, specific answer to a well-formulated experimental question. Moreover, our knowledge of the function of theta rhythms, both on the neural as well as cognitive level, is still developing. This is particularly true of infant research, where the interpretation of the results largely hinges on findings in animal and adult research. For example, no study to our knowledge has yet reported intracranial recordings of theta rhythms in infants, or related the oscillatory activity to the hemodynamic activation of the structures assumed to be involved. Such studies would be necessary to determine whether the scalp-recorded theta oscillations in infants are involved in modulating the effects of the dopaminergic system on hippocampal activity, thereby influencing memory formation, as has been suggested in adult literature (Cohen et al., 2012; Jutras et al., 2013; Orzeł-Gryglewska et al., 2006). Furthermore, although at least one study has performed source localisation analysis on infant EEG data and located the source of scalp-recorded theta activity to the orbital frontal, temporal pole, and ventral temporal areas (Xie et al., 2018), the majority of infant studies do not produce sufficient data for such analysis. Furthermore, due to variation in EEG systems available for studying infants, as well as in how different scalp areas are reported, it is challenging and potentially problematic to discuss commonalities or differences in exact topography of recorded theta activity across studies, which could otherwise offer important insights. Relatedly, while findings from infants tend to parallel those in adults, the exact relationship and the direction of influence between reward expectation, memory formation, and theta oscillations in infants is as of yet unclear.

Last but not least, measuring neural activity in infants comes with several practical challenges. Besides the considerable expense of the equipment and the necessity of bringing families into the lab (rather than e.g. online participation), infant EEG studies typically involve restricting infants' movement, lengthy studies due to the need for repeated measures, and therefore higher attrition rates. Such challenges limit the degree to which this technique may currently be able to broadly inform other disciplines, such as education or machine learning. Nonetheless, we believe this is a promising approach and that its contributions, especially when integrated with other methodological approaches, outweigh such costs.

6. Conclusions

Across many disciplines, it is agreed that active learning is a critical component of human development. However, the mechanisms supporting active learning are not fully understood, thus highlighting the need for the integration of traditional behavioural approaches with tools offered by neuroscience. EEG techniques, and the measurement of theta oscillations specifically, may provide insights into infants' attention, surprise, information seeking, and learning, due to the rich body of literature implicating this rhythm in learning and reward processing on the neural level. Coupling theta measurements with other methods, like eye-tracking or computational modelling, provides unique opportunities to explore open questions in development and to further refine our theories of learning. Through its unique rhythm, theta oscillations may foster coordinated brain activity that supports memory formation and learning; and on a broader scale, its methodological application may foster coordinated research activity that supports theory building across disciplines.

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.

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