

The Importance of Foetuses and Infants in Understanding the Causes and Consequences of Human Social Behaviour

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Keywords:

social behaviour, foetus, infant The aim of this article is to highlight the importance of infant and foetal studies in understanding the causes and consequences of human social behaviour. This article uses examples of infant studies (Azhari et al., 2020; Lloyd-Fox et al., 2013; Parise & Csibra, 2012) to highlight the insights they provide into the developmental timeline of social behaviour and cognition—both typical and atypical. The consequences of these studies extend beyond broadening scientific knowledge, to improving the timing and methods of intervention for autism spectrum disorder (ASD; McDaniel et al., 2020). Foetal studies hold particular value in their contributions to understanding the consequences of human social behaviour, namely speech and language (Carvalho et al., 2019; Kisilevksy et al., 2003; Mampe et al., 2009; Voegtline et al., 2013). These findings about the impact of this behaviour on foetuses have been implemented not only in foetal care scenarios, but also in improving healthcare for hospitalised preterm infants (Filippa et al., 2013). This illustrates the vitality of both infant and foetal studies in the broader study of human social behaviour, principally the proximate causes and consequences.

INTRODUCTION

Foetal and infant studies provide a crucial perspective in understanding the causes and consequences of human social behaviour. Whilst the study of adult and adolescent brains has revolutionised psychology and the study of human behaviour (Atzil et al., 2018; Dunbar, 1998), foetal and infant studies provide a developmental perspective which is easily missed by adult studies. It is true that infant studies are given the due credit for their contributions to the study of infant behaviour (Moszkowski & Stack, 2007; Welch, 2016); however, I suggest that they are underestimated in their explanatory value regarding the causes and consequences of human social behaviour, beyond infancy. From family studies (Mchale, 2007) to educational research (Vygotsky, 1997/2020), infant samples have been widely utilised. Similarly, pregnant mother samples have been used to study foetal development (Dunn et al., 2015; Kisilevsky et al., 2003; Moon et al., 2013; Pierson, 1996) though perhaps less prominent in studies of human behaviour. Having said this, there is a distinct lack of infant and foetal evidence in the study of human behaviour beyond childhood.

I seek to set out how infant brain responses are highly valuable in the proximate explanations of social behaviour, particularly in their neural explanations of social cognition. Similarly, I will use the example of maternal behaviour to demonstrate the importance of studying foetuses in understanding the consequences of human social behaviour. Studying the infant brain provides unique insight into how and when social behaviour develops, as demonstrated by the development of word recognition (Parise & Csibra, 2012) and atypical social processing (Lloyd-Fox et al., 2013). This has real-world implications, particularly in the clinical field. Namely, a better understanding of social development increases the potential for earlier interventions for diagnoses such as autism spectrum disorder (ASD; McDaniel et al., 2020; Bene & Lapina, 2021; Green et al., 2017). Research into foetal behaviour and development provides an equally useful perspective on the consequences of maternal behaviour, though is perhaps less well-evidenced and requires further study (Carvalho et al., 2019; Kisilevsky et al., 2003; Mampe et al., 2009).

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USE OF INFANT BRAIN RESPONSES TO UNDERSTAND SOCIAL COGNITION AND RELATED CAUSES OF HUMAN BEHAVIOUR

Measuring brain responses in infancy can significantly enhance our understanding of the development of social cognition and behaviour. This is because brain activity can be measured objectively whilst infants' perception is manipulated (Hughes et al., 2017). This facilitates useful findings about brain responses to social stimuli (Lloyd-Fox et al., 2013)an essential aspect to consider when studying human social behaviour. Although processing tends to become more sophisticated and specialised throughout development, many of the neural mechanisms underlying infant and adult cognition are similar (Parise & Csibra, 2012), so infant brain responses are highly relevant to the study of adult cognition. Having said this, social behaviours observed in neonates often disappear and later re-emerge, as seen with neonatal imitation and tongue protrusion (Jones, 2007; Nagy et al., 2014). Hence, it cannot be assumed that infant responses, behavioural or neural, can explain adult social cognition or behaviour. To avoid this assumption, longitudinal brain studies (Shi et al., 2011) are effective in tracking the development of cognition throughout development. Infant neuroimaging is also vital in avoiding the underestimation of infant social cognition (Azhari et al., 2020). The methodological challenges of studying infants, explored in the limitations section of this article, are sufficiently overcome using neuroimaging techniques such as electroencephalography (EEG) and functional near-infrared spectroscopy (fNIRS; Wilcox & Biondi, 2015; Stroganova & Orekhova,

2013). This further spotlights the importance of infant brain imaging studies in the understanding of the proximate causes of social behaviour.

Infant word recognition as a proximate explanation for human social behaviour

Word recognition can be viewed as an early sign of language development, which is a key defining characteristic of humans as inherently social animals (Enfield & Levinson, 2020). Therefore, the stage at which word recognition can be observed is a pivotal point in the development of language. This is crucial in the proximate explanation for the uniqueness of human social behaviour. The understanding of words, rather than communication through gestures and other such calls, is largely human-specific (Pinker & Jackendoff, 2005). This can be understood best through the study of infants who provide insight into when this develops-a notable omission of adult studies. The measurement of infant brain responses to semantic word recognition enhances our understanding of social cognition and therefore human behaviour because there is evidence that the same brain activity occurs in both adult and infant word recognition tasks (Parise & Csibra, 2012). Therefore, these measurements are useful not only because they suggest that infants understand more than initially expected, but also in explaining the neural mechanisms of semantic recognition. Parise and Csibra's (2012) EEG study of infant brains provided evidence that infants as young as nine months old have a basic receptive vocabulary. This suggests that semantic understanding has largely developed by nine months-a key insight which could not be provided by adult studies. This study is a successful illustration of the importance of infant brain studies in understanding the development of human social behaviour and communication.

The methodology of this study (Parise & Csibra, 2012), which facilitates its success, is as follows. The study included 28 Hungarian infants assigned to two conditions: mother-speech and experimenter-speech. The researchers selected 15 object labels that two-thirds of Hungarian 1-year-old infants were reported to recognise. These objects were hidden behind occluders, which then dropped to reveal the object when the experimenter or mother said a word either congruous or incongruous with the object. Continuous EEG recordings were taken from the infants to measure the electrophysiological activity in the brain. In the maternal speech condition, incongruous objects elicited N400 event-related-potentials which were significantly more negative in amplitude than congruous objects. This effect was not observed in the experimenter-speech condition. This suggests that these infants could detect the mismatch between the word and object when their mother incorrectly primed the object. This is perhaps because infants tend to trust their mother more than a stranger, so were more surprised by this mismatch, or perhaps they simply paid more attention to mother speech than stranger speech. 12 adults also took part in the study, which further enhances our understanding of social cognition. This is because differential N400 amplitudes were also shown to reflect semantic priming in adults, which indicates that similar mechanisms underlie this aspect of social cognition throughout development. This means that a negative waveform is recorded in both adults and infants roughly 400 ms after the stimuli presentation, suggesting that infants process words using similar mechanisms to adults. This underlines the importance of infant studies, because this comparison reveals that adult-like social cognitive processing is already present in prelinguistic infants, shedding light on its developmental timeline.

This neuroimaging experiment (Parise & Csibra, 2012) provides a robust example of how the measurement of infant brain responses can be used effectively alongside that of behaviour, in order to investigate the development of social cognition. It is true that studying behaviour can be limited by variation and subjectivity more than other measures. For example, only some infants displayed behaviour associated with detecting this mismatch, such as frowning, whereas these brain responses could be measured in all infants. However, infant brain responses can be effectively complemented by other methodologies. For example, the use of eye-tracking technology in the experiment showed that 6-month-old infants tend to have the ability to follow their mothers' instructions to look at the screen (Parise & Csibra, 2012). This highlights that, although

highly effective in understanding social cognition and human behaviour, infant brain recordings are not the only effective measure. With this in mind, the most effective and accurate studies make use of neuroimaging tools in conjunction with other methodologies, such as behavioural and physiological tests. This highlights the importance of varying methodologies in infant studies to fully investigate the development of social behaviour and cognition throughout the lifespan.

The importance of infant studies in the explanation of atypical human social behaviour

Measuring infant brain responses is not only useful for enhancing our understanding of the development of typical social cognition, but also of atypical social cognition and behaviour. This is exemplified by infant studies regarding ASD (Szatmari et al., 2016; Johnson et al., 2015; Lloyd-Fox et al., 2013). Lloyd-Fox and colleagues' (2013) study of infant brain responses provided evidence of reduced neural sensitivity to social stimuli in infants who have a high likelihood of developing ASD. This study included 34 infants between 4 and 6 months old, 18 of which were siblings of children with ASD. These infants were recruited because the heritability estimates of ASD range from 50 to 90% (Tick et al., 2016), so they have a high likelihood of going on to develop ASD themselves. The infants were shown social stimuli, such as a video of a woman pulling faces, and non-social stimuli. Their brain activity was measured with fNIRS. fNIRS is highly suitable for this experiment because it is applicable to infants, unlike functional magnetic resonance imaging (fMRI). While both fNIRS and fMRI have high spatial resolution, fNIRS does not require infants to stay still (Graham et al., 2015). This brain recording method shows the positions of oxygenated and deoxygenated blood using near infrared light, such that areas of the brain that are active can be observed. The use of fNIRS strengthens this study's methodology as it facilitates the accurate study of waking infant brains, where other techniques such as fMRI struggle (Graham et al., 2015). This is vital because, without an effective brain imaging technique suitable for infants, understanding of the development of social behaviour and cognition would be severely limited.

This experiment (Lloyd Fox et al., 2013) found that 3 channels in the posterior temporal cortex (channels 8, 10 and 25) were active in response to social stimuli for low likelihood infants. This differs from infants who were likely to develop ASD, for whom only channel 25 in the right posterior temporal cortex was active. This suggests that the mechanisms of social processing seem to be different in infants who are likely to develop ASD compared to those who are not, as has also been found in several similar studies (Tager-Flusberg, 2010; Nele et al., 2015; Blasi et al., 2015). Understanding of the development of atypical social cognition is crucial for understanding the proximate causes of atypical social behaviour, as is often observed in the behaviours of Autistic individuals (Jones & Klin, 2013; Nakano et al., 2010; Hattier et al., 2011). Therefore, this study exemplifies how measuring infant brain responses to social stimuli can provide significant insight into atypical development of social cognition and subsequent behaviour.

Having said this, from this experiment (Lloyd Fox et al., 2013) alone, we cannot establish whether these differences in neural activation are due to differences specifically in social cognition, or in other cognitive domains such as attentional mechanisms. This does not detract from the importance of infant studies; it simply highlights where infant and non-infant studies are effective in complementing each other. Other infant studies have suggested that this difference in neural activity is due to impaired attention (Jones & Klin, 2013; Elsabbagh et al., 2009; Jones et al., 2016). These studies have been supported by studies of children and adolescents (Mundy & Sigman, 1989; Pellicano, 2010) which suggest that these differences in neural activation are associated with joint attention and mentalising impairments. This corroborates the initial findings of Lloyd-Fox and colleagues (2013), strengthening the association between atypical social behaviour and impaired social cognition, specifically joint attention and mentalising. Evaluating infant studies alongside complementary non-infant studies demonstrates the vitality of studying infants in understanding the onset of atypical social behaviour. Whilst studies with child-samples could find similar results, infant studies are unique

in their discovery of the chronology of atypical social behaviour and neural activity. That is, infant studies (Lloyd-Fox et al., 2013; Elsabbagh et al., 2009) suggest that this atypical neural activation is present as early as four months old.

The advantages of infant, over adult, studies

The most obvious advantage infant studies hold over adult studies is their scope for a longitudinal perspective, from birth. Unlike adult studies, infants provide insight into when in infancy communication develops—both typical and atypical. Crucially, the use of infants rather than adults in the above studies facilitates research into the early signs of ASD and other disorders, working towards opportunities for earlier diagnoses and potential models of prediction. Whilst both adult and infant studies could conclude that particularly high brain activation in certain areas is associated with ASD, infant studies have the advantage of finding reliable predictors of ASD before behavioural symptoms are presented, rather than drawing associations between pre-existing diagnoses and following brain activity (Magiati et al., 2014). This is arguably more noteworthy than studies of adult brains, because of the real-world impacts; the ability to reliably predict such disorders could enable more effective support programmes earlier.

For example, McDaniel and colleagues (2020) found that toddlers receiving a pivotal response treatment package performed significantly better than controls in reciprocal vocal tasks after 24 weeks of treatment, with a moderate effect size of 0.69. This treatment package consisted of 180 hours of parent-led and clinician-led at-home interventions. These interventions emphasised the inclusion of behavioural interventionists in child-led play with child-preferred toys, with the aim of developing communication and vocalisation (Gengoux et al., 2019). This correlation suggests these pivotal response interventions are associated with improved social communication and behaviour. Similarly, Bene and Lapina's (2021) meta-analysis of sibling-mediated interventions found an overall effect size of 0.83 for the 16 studies analysed, which is statistically large. However, it is worth noting that there is insufficient evidence regarding the long term effects of these interventions, as there is a notable lack of follow-up studies in the literature. Therefore, whilst it has been suggested that pivotal response treatment packages are effective interventions, longitudinal studies are warranted to strengthen this conclusion. Other effective modes of intervention include parent-mediated interventions of social communication (Green et al., 2017), and group social skills interventions (Wolstencroft et al., 2018). The timing of these interventions is crucial (Koegel et al., 2014), highlighting the unique importance of infant studies in studying social behaviour. This is because they have provided an insight into when atypical social cognition develops and therefore when interventions are most effective (Koegel et al., 2014), as well as illustrating the overall benefits of interventions for high-likelihood ASD toddlers (McDaniel et al., 2020; Bene & Lapina, 2021).

USE OF FOETAL RESPONSES TO UNDERSTAND THE CONSEQUENCES OF HUMAN SOCIAL BEHAVIOUR

Having explored the significance of infant studies in investigating the causes of social behaviour, through the case of ASD, the focus of this article now turns to the importance of foetus studies in studying the consequences of social behaviour. There is evidence to suggest that social behaviour influences foetal sensory capacities (Carvalho et al., 2019; Kisilevksy et al., 2003; Mampe et al., 2009), demonstrating the importance of studying foetuses in understanding the consequences of maternal social behaviour. This section of the article will use the examples of prenatal exposure to a maternal voice and to a specific language to demonstrate how exposure to social behaviour facilitates the specialisation of auditory capacities. This highlights the influence of social behaviour, even before birth—a perspective which adult studies are unable to take.

The importance of studying foetal responses in understanding the consequences of maternal speech One of the most common social behavioural influences on foetal auditory capacity is the effect of hearing the mother's voice whilst in utero (Voegtline et al., 2013; Jardri et al., 2012; Kisilevsky et al., 2009). This highlights the influences which maternal social behaviour has on foetuses, illustrating the broader importance of social behavioural influences, even before birth. Assuming normal health of the mother and foetus, foetuses should have the capacity to hear at around 20 weeks (Hepper & Shahidullah, 1994). However, hearing their mother's voice is argued to provide foetuses with the opportunity to distinguish between voices, perhaps specialising their capacity to process sound. This is supported by empirical evidence (Jardri et al., 2012) which has found different areas of activation within the temporal cortex upon hearing the maternal voice, compared to female controls. This demonstrates the importance of foetal studies in understanding the consequences of social behaviour; this specialisation of auditory processing seems to be influenced by social behaviour, which would be neglected in the absence of foetal studies.

This influence of social behaviours before birth has been demonstrated empirically (Carvalho et al., 2019; DeCasper et al., 1994; Voegtline et al., 2013). Voegtline and colleagues' study (2013) of 74 gestating women concluded that foetuses turn their head towards their mothers' voices, significantly more than expected due to chance. There was a 50 minute baseline recording of the foetuses followed by a 2 minute read-aloud section, in which the mothers read from a neutral passage about nature. Foetal heart rate and movement were measured by a Doppler transducer on the mother's abdomen, sampling both measures at 200 ms intervals. The reliability of the study was increased by the exclusion of 5 individuals, due to high heart rate variability. The results observed were that foetal movement increased significantly in the read-aloud section. Additionally, the foetuses seemed to orient towards the mother. The mean heart rate showed a startle response when the mothers started talking, followed by a decline, perhaps as the foetuses were calmed. This suggests that the foetuses had the ability to distinguish between their mothers' voices and the voices of strangers, which would not be possible if they had not been exposed to the maternal voices. It could be argued that these results (Voegtline et al., 2013) do not prove that it was the owner of the voice who engaged the foetuses, as they could have simply been responding to sound. However, 42 of the individuals stayed awake in the baseline period, surrounded by strangers' voices, and the difference in movement and heart rate was still significant when the mother started speaking. Therefore, although a flawed study, it has been suggested that near-term foetuses respond disproportionately to their mothers' voices in a crowd of strangers, in terms of both physiological and behavioural responses. This serves to reiterate the considerable importance of foetal studies, due to the real-world consequences of this research.

Along with other foetal studies demonstrating the influence of maternal speech (DeCasper et al., 1994; Carvalho et al., 2019), this research has not only enhanced understanding but also been associated with clinical breakthroughs (Filippa et al., 2013). The concept of maternal speech and social behaviour influencing foetal capacities has been extended and applied to infants, to be implemented into the NICU. Maternal speech and singing have been shown to have significant effects on hospitalised infants' physiological states, improving their oxygen saturation levels and overall stability (Filippa et al., 2013). This illustrates the importance of foetal studies in understanding maternal social behaviour, not only because of the insight provided into the consequences of maternal behaviour, but also the real-world impacts of these insights.

Having said this, it is difficult to investigate the effects of hearing a mother's voice on foetal sensory capacities because this is almost universally present in pregnancy, so there is a lack of data about foetal sensory capacities in the absence of maternal voice exposure. However, it remains highly plausible that such social factors do influence foetal auditory capacities, especially due to the presence of several studies with similar robust findings (Kisilevsky et al., 2003; DeCasper et al., 1994; Carvalho et al., 2019).

The importance of foetal responses in understanding the consequences of native speech

There is evidence that the language a foetus is exposed to in utero influences foetal capacities in a similar way (Pino, 2016; Moon et al., 2013; Carvalho et al., 2019). Carvalho and colleagues' (2019) study provides evidence to suggest that the native language a foetus is surrounded by influences foetal auditory capacities through specialisation. This evidence alone would not be enough to support this claim because its limited methodology means that maternal voice was a confound. However, Mampe and colleagues' (2009) study provides much stronger corroborating evidence. The analysis of 60 neonates, 30 exposed only to French in utero, and 30 to German, showed that the rising and falling melody arcs (i.e., prosody) of neonatal cries are significantly reflective of the respective languages. This indirectly supports the argument that social influences affect foetal auditory capacities. This is because, similarly to exposure to maternal voice, exposure to a particular language provides foetuses with the opportunity to specialise their auditory capacities and tune in to particular sounds. Mampe and colleagues' (2009) evidence supports this because it suggests that not only can foetuses distinguish their native language from others, but also that they can use this as an opportunity to develop their memory and general learning capacities (Moon & Fifer, 2000), which they otherwise might not be able to. This demonstrates how social behaviour such as spoken language has consequences for foetal capacities. Therefore, foetal studies are significant in drawing attention to the impacts that social behaviour has, and illustrating the general trend that increased exposure to social influences seems to improve and specialise foetal sensory capacities (Carvalho et al., 2019; Mampe et al., 2009).

The importance of foetal, rather than adult, studies

The focus on foetuses as opposed to adults in these studies is critical because the consequences of human behaviour on foetuses have clinical implications, such as the application of foetal benefits of maternal speech to preterm infants (Filippa et al., 2013). Moreover, the foetal studies discussed illustrate the general trend that increased exposure to social behaviour has positive impacts on foetal capacities, as exemplified by the positive influences of maternal and native speech (Voegtline et al., 2013; Mampe et al., 2009).

DISCUSSION

Summary

Both infant and foetus studies have provided novel insights into the proximate causes and consequences of human social behaviour. Infant studies are particularly powerful in deciphering the timeline of social behaviours, both typical and atypical (Parise & Csibra, 2012; Lloyd-Fox et al., 2013); whereas, foetus studies provide evidence for the consequences of adult social behaviour, including maternal speech and its language (Lalande et al., 1986; Mampe et al., 2009; Kisilevsky et al., 2003; Voegtline et al., 2013; Carvalho et al., 2019). Studies involving infants and foetuses pave the way for future research. Infant studies provide a well-supported basis for research into predicting diagnoses and how support can be made more widely available before diagnosis is possible. Foetus studies, although perhaps more challenging and less well-evidenced than infant studies, have provided feasible hypotheses about the consequences of adult behaviour on development starting from the prenatal period. This is on top of the clinical implications in terms of utilising social behaviour (Filippa et al., 2013). Further research is warranted to investigate the consequences of more general social behaviours, such as the type of speech a foetus is exposed to. This is particularly important because social behaviours are more difficult to control for than specific, physical, and more well-researched behaviours, such as maternal alcohol intake (Erb & Andresen, 1978).

Limitations

Despite the effectiveness of infant brain recordings in the study of social cognition and behaviour, it could be argued that the brain structure changes too rapidly in infancy for these to have any useful implications (Paterson et al., 2006). However, the brain has high plasticity and

continues to change into adulthood (Bruce & Echemendia, 2003), so having infant measurements can be equally useful for understanding the development of cognition, regardless of how long the findings are applicable for (Lebel & Beaulieu, 2011). Understanding the developmental timeline of social cognition and behaviour would be near-impossible without infant studies, and has considerable implications for atypical social cognition interventions (Koegel et al., 2014) as well as general scientific understanding (Nakano et al., 2010).

Having said this, it is worth noting the methodological difficulties of studying infants, and how these limit the findings of infant studies. The high measurement errors caused by the often seemingly spontaneous behaviour of infants (Byers-Heinlein et al., 2021) are associated with low statistical power, limiting the effect sizes of infant studies. Although measures of brain activity such as fNIRS are more reliable (Azhari et al., 2020), the study of infant behaviour is limited by the infants' inability to verbalise or explain their behaviour. This leads to less certain conclusions (Zettersten et al., 2022) and, as previously stated, higher measurement errors. Furthermore, the measurement of atypical infant behaviour is inherently challenging due to the overlap with behaviours seen in typical infant development (Zwaigenbaum et al., 2007). This is especially true regarding sensory stimulus-seeking and avoiding, which presents itself differently between individuals, and for which there is little data from typically developing infants. This highlights the necessity of further research into infant behaviour and cognition, not only because of the significant insights provided by previous infant studies, but also because of the need for more developmental data for comparison and replication. These methodological difficulties of studying infants do not take away from the huge importance of infant studies in understanding the proximate causes of social behaviour. They simply spotlight the need for further studies to support the current findings and to compensate for the high measurement errors (Zettersten et al., 2022).

The study of foetus responses to social influences is also limited due to the methodological difficulties and inconsistencies in foetus studies. Dunn and colleagues' (2015) review of foetal studies reported significant variation in foetal physiological and behavioural responses, upon presentation of the same stimuli. This was put down to varying study designs and methodologies, but still raises the question of reliability. It is also worth noting that the development of foetal auditory capacities is relatively canonical (Slater, 1998), so it remains a difficult task to prove beyond doubt whether social influences and human behaviour do influence foetal auditory capacities. This is particularly true because many of the human behaviours investigated, such as maternal speech, are almost universal in gestation. Therefore, it remains a challenge to find a control group to compare results to over a longer period of time than a single experiment. Nonetheless, consistent use of electrocardiograms, fMRIs and ultrasounds (Azhari et al., 2020; Byers-Heinlein et al., 2021; Graham et al., 2015) have provided evidence to suggest that these social influences, at least in the short term, have some effect on foetal ability to process sound. Therefore, it can reasonably be concluded that the consequences of some social human behaviours, namely maternal speech and language, include influences on foetal development. Moreover, the measurement of foetal physiological responses can be made more reliable by the application of certain algorithms. These process waveforms from the Doppler ultrasonic method of measuring foetal heart rate, for example (Tuck, 1981). This increases the reliability of foetal response measures, minimising the aforementioned limitations. As such, these methodological limitations do not render foetal studies futile. Converging evidence from the studies discussed in this article suggest that the conclusions are reliable-these conclusions being that human social behaviour influences foetal capacities. Therefore, foetal studies remain paramount in understanding the consequences of social behaviours, such as speech and language.

CONCLUSION

To conclude, infant studies can significantly enhance our understanding of the proximate causes of human social behaviour. This is because they can provide substantial evidence for the developmental timeline of social cognitive abilities, such as semantic word recognition. These measurements can also develop our understanding of atypical social cognitive development, such as is observed in individuals with ASD. This in particular could be more useful to psychologists than adult studies in aiding models of prediction for ASD, as well as evaluating interventions. It has been argued that infant studies fall short in terms of their high measurement errors (Zettersten et al., 2022). However, this is a reflection of methodological difficulties, and does not warrant the neglect of these studies.

In terms of foetus studies, evidence suggests that social behaviour can influence foetal sensory capacities (Carvalho et al., 2019; Mampe et al., 2009; Voegtline et al., 2013). Human social behaviour such as maternal voice and native language exposure seem to have some effect on foetal capacities, although the mechanisms of these effects remain debated. Much of the debate around whether the current evidence is strong enough to fully support this claim stems from difficulty measuring exactly what and how foetuses can hear and process sound (Gerhardt & Abrams, 1996). Therefore, as technology develops, this could be a ground-breaking avenue for new research. Furthermore, the application of foetal studies' findings to clinical settings (Filippa et al., 2013) has the potential to be further extended, to utilise the effects of maternal social behaviour on both foetuses and infants. These positive effects show the potential to improve care for hospitalised preterm infants, as certain maternal social behaviours seem to stabilise infant oxygen saturation levels (Krueger, 2010; Filippa et al., 2013). This effectively exemplifies how both infant and foetal studies are crucial in understanding the causes and consequences of human social behaviour, as well as having novel real-world impacts.

Interdisciplinary Commentary

B I O L O G I C A L A N T H R O P O L O G Y

Reflecting the full breadth of human variability

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Human behaviour is variable across different populations, a product of diverse social, cultural, and biological factors. Most studies have nevertheless relied on a sample of subjects which does not reflect the full diversity of our species and does not provide a good basis for making general assumptions about human behaviour. Corrections are being made, including an increased focus on the development of different behaviours in foetuses and infants, as outlined in the article. Whilst important in providing novel insights into human behaviour, it is imperative that these studies also include subjects from a diversity of populations to ensure that the full breadth of human variability is reflected. Only then can we assume that our models are reflective of human behaviour in general, rather than of only a limited selection of populations.

Introduction

Humans are behaviourally complex. Understanding both what leads to certain behaviours and the consequences of those behaviours is not only of epistemic interest but can also have real-world impacts. As an example, the author of the above article argues that understanding the neural processes behind autism spectrum disorder (ASD) in high-risk infants is invaluable for producing models capable of predicting ASD as well as providing individuals with the necessary intervention to prevent or alleviate any negative consequences related to atypical social cognitive development. However, the studies cited in the article focus on a narrow sample of subjects derived from WEIRD (Western, Educated, Industrialised, Rich, and Democratic) populations (see Henrich et al., 2010). Whilst a focus on infants and foetuses for understanding the causes and consequences of human behaviour is indeed necessary, it is essential to ensure that the novel insights gained from these studies are not generalised without accounting for the high variability across populations, both within and beyond WEIRD societies (Apicella et al., 2020). This is not just an issue for foetal and infant studies but indicative of the psychological sciences in general (Barrett, 2020; Henrich et al., 2010; Pollet & Saxton, 2019; Rad et al., 2018). The overrepresentation of WEIRD societies needs to be resolved to ensure that we produce models of human behaviour that reflect the full diversity of our species and ensure that potentially unethical consequences do not materialise for underrepresented groups, due to unsupported generalisations made on the basis of a WEIRD sample population (Brady et al., 2018; Keller, 2018). This attention to understudied populations is particularly important for studying early neurodevelopmental outcomes, too (Hilton, 2023).

Why we should not just study WEIRD populations

Different evolutionary pressures exist for different populations across the globe and, consequently, populations have evolved differentially. A classic example is that of the sickle cell trait, found within several sub-Saharan populations and provides strong protection against malaria for heterozygotic carriers of a number of associated alleles (Luzzatto, 2012). This is well-explained by evolutionary adaptation, as the populations where this trait is present live in areas where malaria is endemic. Thus, it evolved within these populations since it made individuals with it fitter in their specific environments; whereas it was not selected for in populations inhabiting areas with a lower prevalence of malaria, due to its negligible fitness benefits relative to the high chance of fatality in homozygotic carriers of the allele, in whom it causes sickle cell anaemia. Like many other traits across the world, the sickle cell trait seems to have emerged due to environmental conditions.

Adaptations are seldom only influenced by one factor, but are rather often the product of intertwined cultural, social, and ecological factors. An example is human olfaction. Sorokowska and colleagues (2013) demonstrated that the Tsimane' from Bolivia, a group which lives in a rainforest environment, were better at picking out smells than their industrialised, German control subjects. Yet the difference in olfactory capacity is also reflected cognitively between groups. The hunter-gatherer Jahai are capable of abstracting smells the same way that WEIRD populations abstract colour (e.g., red, green, and blue; Majid & Burenhult, 2014). This is in stark contrast to speakers of most Western languages who describe smells evaluatively (rancid, putrid, pleasant) or by referring to something else (floral, sweaty, or like coffee; ibid.). Not only can the Jahai abstract scents, but they can abstract and name scents and colours with equal proficiency (ibid.).

To substantiate whether different olfactory capacities could be caused by socio-cultural processes, Majid and Kruspe (2018) compared the ability to name odours as compared to colours in the horticulturalist Semelai and hunter-gatherer Semaq Beri. Both peoples speak closely related languages and live in a similar environment on the Malay Peninsula. The results showed that the Semelai struggled to name odours but excelled at naming colours, whereas the Semaq Beri were adept at naming both. Since ecology and language could be ruled out as explaining factors, the researchers linked olfactory capacity and the ability to abstract odours with the respective subsistence patterns of the two groups (see Majid, 2021). It may be that being able to name odours provides the Semaq Beri with increased fitness in their ecological niche as hunter-gatherers since it may allow for more precise plant and animal identification and safer communication of this within the group. Across human populations, different pressures lead to multiple trajectories, influencing our bodies, culture, as well as cognition in myriad ways that should not be ignored.

Yet differences should not be overstated. Humans are still mostly culturally, biologically, and socially similar, and the idea that races can explain intrahuman variation has been falsified by decades of anthropological research (Fuentes et al., 2019). Nevertheless, failing to recognise and engage with human variability risks producing models that only reflect a fraction of reality at the cost of under-represented groups (Hruschka et al., 2018). The idea that there are certain universals in human nature (Brown, 2004) becomes problematic since many of these so-called universals may not be derived from samples representing the totality of humanity. In an attempt to highlight this disparity, Henrich and colleagues (2010) proposed that we move beyond WEIRD societies which have hitherto been overrepresented in studies of human behaviour within the social sciences. By contrasting human populations that are socially, culturally, and ecologically dissimilar, it becomes possible to produce models of human behaviour that account for higher variability.

This should not be taken to suggest that human societies can be understood in a simple WEIRD/non-WEIRD dichotomy. Such an approach risks the "exoticizing and othering of research participants" (Clancy & Davis, 2019, p. 172) due to the implicit biases present in researchers and reviewers who are often themselves from WEIRD societies. This dichotomous thinking can also obscure intragroup variation within the populations of interest, whether industrialised Western or Amazonian hunter-gatherer societies (Clancy & Davis, 2019). But as a heuristic for highlighting differences in lived experiences and behaviours across societies, the WEIRD acronym remains useful (cf. Hilton, 2023 and accompanying commentaries). With that in mind, researchers should probe potential variability across societies and within them, and recognise their own biases as individuals from myriad, distinct societies rather than simply focus on those of their test subjects. If this is systematically done, our models of human behaviour and biology and, consequently, treatments and interventions taken on the basis of these, can better account for the full diversity of the human experience.

Conclusion

The focus on WEIRD societies has produced models and frameworks of behaviour that are focused on a fraction of humanity. By accepting the fact that both societies and their people develop differently due to a combination of social, cultural, and biological factors, it becomes possible to better account for cognitive, physiological, and behavioural variation and develop more integrated approaches in the future. This is important to ensure that remedial and preventive action meant to alleviate the negative consequences of different traits and conditions works accordingly for all individuals (Brady et al., 2018; Keller, 2018).

To improve our models of human behaviour, it is essential that the biassed results derived from the limited focus of many studies are resolved in the future. These biases are not just derived from a lack of focus on differential experiences across populations but also within them. As highlighted in the above article, infant and foetal studies are well-placed to begin alleviating some of these biases by focusing on novel aspects of human behavioural development, but this needs to be complemented by a continued focus on differences between populations. Understanding whether this plays any role in behavioural development beginning in the prenatal state requires that the broadest possible focus on populations from across the world is applied. There are many difficulties in working with diverse populations, and these are only heightened by the difficulties present in working with foetal and infant subjects discussed in the article. But if we aim to truly understand the causes and consequences of human behaviour, it is imperative that the sample studied is representative of the full diversity of humankind, not just within populations but also across them. Only then is it possible to talk of a truly human scientific endeavour.

PSYCHOLOGY

Influence of foetus and infant studies on sociolinguistic paradigms

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Increased data on human ontogeny is of vital importance to better resolving debates within both linguistics and social anthropology. Foetus and infant studies are helping to better understand how individuals acquire linguistic abilities and learn languages, which in turn allows linguists to better test the claims of universal grammar. Similarly, anthropologists have observed great cross-cultural variation in the importance of the concept of *face*, so understanding how one develops a sense of this concept early in life may elucidate how the variation observed in adults comes to be. These current gaps in our understanding of linguistic and cultural phenomena highlight the cross-disciplinary importance of foetus and infant studies.

Introduction

As the author of the above article mentions, it is vital to study foetuses and infants as there are significant lacunae in the studies of this particular group of people. Foetuses and infants undergo significant changes in the development of their brain and some of those could be crucial in the emergence of "atypical social cognition and behaviour" (Rigby, 2023). Speaking generally, studying foetuses and infants provides us with insights into what makes us human and how we develop into the individuals we grow into later in life. Since this period of development is pivotal, it is interesting to consider it through a social anthropological lens and how it influences human behaviour. This commentary stems from the discussion of speech in the given article and will discuss the ways in which studies of very young children can influence various sociolinguistic paradigms.

How foetus and infant studies can benefit the debate on universal grammar

One of the most notable sociolinguistic paradigms that one thinks of when thinking about foetuses and infants is the notion of innate or universal grammar. The basic idea behind this paradigm is that language and the conventions associated with language are innate, and children are born with the ability to construct sentences and learn language (Cowie, 2017).

Many philosophers and psychologists pondered this issue for ages, as the question of where language comes from is one of the most fundamental questions of humanity. In modernity, this theory is mostly associated with Noam Chomsky (1959) and his refutation of Burrhus Frederic Skinner's idea of language being learned, instead of innate. Chomsky (1959) contradicts Skinner's opinion that language is based on behavioural dispositions and is produced as a response to particular stimuli and the various conventions of language, thus being acquired by children as they navigate the world while they grow. Cowie (2017) explains that Chomsky argues for language to be stimulus independent, meaning that there does not have to be a correlation between language and the stimulus from the environment, as people can say things which are independent from the outside world but purely come from one's mind. Thus, it is extremely fascinating to consider brain studies of infants and foetuses to attempt to find a resolution to this debate. In this way, we may be closer to understanding how people communicate and how language operates, which will provide us with a deeper understanding of ourselves.

How foetus and infant studies can benefit the debate on universal *face*

Another sociolinguistic field that could benefit from the study of young children is the study of *facework*. Goffman (1967) first used the sociolinguistic term *face* in his research on facework and related rituals in social interaction. He characterises face as a social asset that one individual possesses and that others recognize. Goffman (1967) for example, defines saving face as "the process by which the person sustains an impression for others that has not lost face" (p. 9). Thus, facework is a theoretical framework that describes how individuals engage with their own and others' faces. Goffman (1967) suggests that the notion of face is universal as he claims: "members of every social circle may be expected to have some knowledge of facework and some experience in its use" (p. 13).

Similarly, the most famous followers of Goffman's theory, Penelope Brown and Steven C. Levinson (1987) established face as "basic wants that every member of society desires" (p. 312); however, more contemporary sociolinguists like Michael Haugh (2013) argue against the universal notion of face. For instance, when analysing non-Anglo-Saxon contexts, the face does not seem to function solely for the sake of the individual, but may also be a phenomenon shared by a group of people. Thus, for instance "in Thai, in many cases 'consideration for others' feelings' is foregrounded over and above any concern for their personhood or self-image" (Haugh, 2013, p. 63). Therefore, it would be very interesting to study infants of various nationalities and how they perceive themselves in social interactions. Since young infants would not have as much social interaction and are not affected by accepted social norms as much, it could help us gain an insight into whether the notion of face and maintaining one's face is a universal concept or not.

The author of the above article notes some limitations in studies of infants and foetuses, namely methodological concerns such as the results from foetuses and infants being inaccurate due to the high plasticity of the brain; however, another concern that may arise in the studies of young children is the notion of consent. Young foetuses and infants are not able to provide the researchers with informed consent, and if procedures such as electroencephalography (EEG) and functional neuro-infrared spectroscopy (fNIRS) are proven to be uncomfortable or even harmful to the baby, the morality of the study may be thrown into question. This could be one of the reasons why legal guardians of the child who give consent for their baby to be studied may be wary about putting their child into a situation that may be out of their control when their infant is still frail. Thus, conducting research on infants and foetuses may be more problematic because of the issue of informed consent.

Conclusion

Despite the limitations, it is still important to study foetuses and young infants as they may provide us with invaluable knowledge on the causes and consequences of human social behaviour. Since babies are not exposed and affected by the social conventions of the society they were born into as much as adults, studies on young children can provide answers to many questions regarding the innateness of linguistic and societal conventions. One of those questions is whether ideas of universality in society, namely universal grammar and universal face, are true. Since these questions deal with social norms, it is difficult to understand whether they are truly innate and universal, or develop as a result of outside stimuli. For this reason, foetus and infant studies are still important to conduct.

BIOLOGICAL SCIENCES

Anatomical insights into early human cognitive development

Yuankai He Christ's College, University of Cambridge, United Kingdom Though extensive studies have investigated the functional significance of foetal cognitive development, quests for its neural substrate are rather limited by the availability of study techniques. Several novel technical developments in structural neuroimaging in conjunction with ex vivo high-resolution magnetic resonance imaging (MRI) and histological studies are providing increasing detail of the structural development of the foetal human brain. Meanwhile, whilst the application of in utero functional imaging is limited by foetal movement, investigations into the immediate response to sensory stimuli are seeing much progress which can be in turn correlated with the structural findings. Though methodological diversity in neuroimaging might account for discrepancies between different imaging studies, a reliable reference of the foetal brain structural development provided by histology, ex vivo MRI complemented by in vivo MRI might catalyse more studies at the interface of the early anatomical and functional brain development.

Delineating the structural development of the foetal brain

The foetal brain is a region of rapid anatomical development and changes are observable on a weekly basis (Vasung et al., 2019). In order to better understand this rapid process, evidence from different approaches need to be collated.

T_1 - and T_2 -weighted magnetic resonance imaging (MRI)

 T_1 - and T_2 -weighted MRI have the potential to distinguish between tissue types and are commonly used for volumetric measurements of the brain. One challenge to *in utero* imaging is localisation and movement correction for the foetus. Recent technical advancements into fast MRI techniques and image pre-processing protocols have thus far enabled *in utero* imaging by sending a fast localiser sequence and then capturing an initial T_2 image as a template for later registration (Manganaro et al., 2017).

Utilising a similar protocol, a large-scale normative study (Andescavage et al., 2017) established that cortical development starts at around 18 weeks into gestation, with deep brain nuclei volume increasing roughly linearly, white matter (WM) growing at decreasing rate, and cortical grey matter (GM) growth accelerating throughout gestation. Hence, the GM/WM ratio and GM/total brain volume ratio show a U-shaped curve during gestation. This result echoes previous finding that cortical folding gradually increases throughout gestation, i.e., cortical surface increases faster than the brain volume. More specifically, the Sylvian fissure is first to develop (18-19 weeks), while other cortical folds generally start to develop exponentially at around 24-25 weeks (Habas et al., 2012). Of particular interest is the correspondence between the U-shaped GM/ brain volume ratio and the U-shaped development in performance in cognitive tasks commonly implicated in human infants. This correspondence should be further investigated with correlational or functional imaging studies (Loucks & Sommerville, 2018; Marcovitch et al., 2008; Pattwell et al., 2012).

Diffusion weighted imaging and diffusion tensor imaging

Diffusion-weighted imaging (DWI) is a variant of MRI that measures the diffusivity constant of protons in a particular direction. By combining diffusion-weighted data in several directions, one can infer the optimal diffusion direction of protons at any given voxel in diffusion tensor imaging (DTI). Since protons diffuse easier within an axon than across the axon membrane (i.e., the diffusion tensor is anisotropic), axon tracts can be inferred from DWI images (Poupon et al., 1999).

Various *in utero* DTI studies have converged on a critical period for axonal tract development at around 23–42 weeks, where, importantly, developmental onset of different axonal tracts is asynchronous (Bui et al., 2006; Dubois et al., 2014; Khan et al., 2019; Marami et al., 2017; Ouyang et al., 2019). Lateral intra-hemispheric connections are first to emerge at around 19 weeks (Ouyang et al., 2019), whereas the corpus callosum development starts from the anterior end (genu) at about 22 weeks and then progresses to the posterior end (splenium) at ~25 weeks (Khan et al., 2019). The latest to develop are associational axonal tracts (30–35 weeks) which correspond to the late functional development of higher associations (Mitter et al., 2015; Yu et al., 2016). The developmental heterogeneity across different WM tracts continues into the 3rd trimester, with one recent study suggesting a halt in WM development in several tracks that develop early (Hooker et al., 2020). To summarise, whilst the number of foetal DWI studies is limited by technical constraints, initial results demonstrate that the WM development of the foetus also shows a staged pattern that might also represent the order of functional development, from local integration to bilateral integration and then to higher associations, boding well for a structural-functional convergence.

Ex vivo histological studies

Histological studies have always been considered the "gold standard" for anatomical investigations, given the extensive range of study techniques and ability to produce high resolution images; however, the scope of human foetal histological studies of brain structure is highly limited by the number of available healthy samples, usually from *in utero* dead or aborted foetuses. Hence, these studies serve as valuable references for neuroimaging approaches.

One significant trend identified in several histological studies is the rather staged development, from general enlargement to region-specific growth. The first structures of the brain are visible at 10 weeks (ventricles, ventricular, subventricular zones, and cortical plate), whilst early development is characterised by rather uniform, globular enlargement with layer specifications, regional-specific development (including the distinction between basal ganglia and diencephalic nuclei), and cortical plate thickening starts at ~17 weeks, a finding cross-validated by ex vivo MRI imaging (Wang et al., 2015). This finding closes a gap of knowledge in *in vivo* imaging studies that does not attain this high resolution at early gestational stages. Development during the 3rd trimester agrees with the findings of T_1/T_2 -weighted MRI (above) in the exponential cortical growth, with the initial in-folding of the brain observed at 19 weeks, and other cortical infoldings only observable at 26-28 weeks. The rate of infolding increases so significantly that, by 31 weeks, all main sulci of the brain are observable (Kostović & Judaš, 2010). Importantly, histological studies also offer a mechanistic explanation for this developmental pattern: axons of thalamocortical projections terminate in the subcortical plate before 26 gestational weeks and progress in a deep superficial order, reaching the cortical plate at 28 weeks and layer IV at 34 weeks; whereas refinement of synapses, inter- and intra-hemispheric synchronisation are observed by 37-38 weeks (ibid.; Kostović & Rakic, 1990). Hence, the formation of synaptic contacts likely explains the exponential cortical expansion in MRI studies.

A recent histological study focused on WM fibre development has provided complementary evidence for DTI-based studies, confirming the apparent sequence of fibre tract when these axonal tracts grow extensively: superior and inferior fronto-occipital fasciculi (~17 weeks), corpus callosum, fornix and anterior commissure (~23 weeks), cingulum, and uncinate fasciculus (~32 weeks). However, the initial appearance of these WM tracts in the dissection is much earlier than in DTI imaging, with pioneering axons arising at 13–14 weeks (Horgos et al., 2020), highlighting the limitation of DTI in detecting the initial axonal tracts.

Overall, the good alignment between histological and *in vivo* imaging studies provides a firm foundation for function–structural correlations; however, the limited resolution and noise natural to neuroimaging still poses a challenge to early-stage structural investigation. New high-resolution and true-fast imaging techniques (Manganaro et al., 2017) might eventually produce more convincing findings that match the histological reference.

Relating foetal anatomical to functional brain development

Though functional neuroimaging for foetuses is possible, a reliable fMRI protocol for foetuses is yet to be developed. A major challenge for

functional imaging is motion correction for the foetus (Studholme, 2011) and neuroimaging is mainly limited to stimulus-correlated blood-oxygen-level-dependent (BOLD) signals, electroencephalography (EEG) and magnetoencephalography (MEG), where single volumes are taken. A main focus of these studies is the development of the auditory system and its projections which is known to be influenced *in utero* by external stimuli (addressed in the commented article). Hence, auditory development is used as an example to illustrate the functional development of the foetal brain and relate to the structural development.

Auditory stimulated response in foetuses was first recorded in 1985 utilising a neuromagnetometer placed onto the maternal abdomen, revealing bilateral activation of the temporal lobe in response to an auditor stimulus at ~130 ms post-stimulus (Blum et al., 1985). However, due to the limited number of channels and low spatial resolution, the signal-to-noise ratio was quite low. Subsequent studies have improved in both regards and by now dipole-fitting algorithms have allowed the localisation of in utero auditory stimulated MEG signals to the anterior temporal cortex (Bisgin et al., 2021). These technological advancements have set the stage for a series of longitudinal studies, which all agree on the emergence of auditory stimulated responses before 27 gestational weeks (though some negative results are reported at 28-30 weeks), but draw diverging conclusions about the development of response latency (either increasing or decreasing, all within the range of 100-200 ms; Draganova et al., 2007; Eswaran et al., 2007; Holst et al., 2005; Sheridan et al., 2010). Supporting evidence of in utero auditory stimulated temporal responses were found from two fMRI studies which show a fairly uniform increase in BOLD signal in the primary auditory cortex (superior temporal lobe) at >37 gestational weeks (Jardri et al., 2008; Moore et al., 2001); however, these cross-sectional studies are yet to be complemented with longitudinal studies.

In general, the developmental pattern of the stimulus response seems concordant with the structural development in the foetal brain, with the superior temporal sulcus developing at 25 gestational weeks (Habas et al., 2012). The highly localised BOLD activation at >37 gestational weeks might also be explained by the synaptic refinement around that time (Kostović & Rakic, 1990); however, it should be noted that the onset of cortical auditory response is observed a week before the thalamocortical projections reach the cortical plate (28 weeks) and well before they synapse onto layer IV (34 weeks; Kostović & Judaš, 2010). Recalling that the foetal brain develops very rapidly, this one-week discrepancy cannot be ignored and neuroimaging evidence should be treated with more caution in light of the "gold standard" histology findings. In addition, there seems to be a publication bias looming over the functional characterisation of foetal audition, calling for more work to be published about the lack of brain response to auditory stimuli before a putative critical onset of auditory function.

Implications for foetal cognitive studies

Studies of human foetal cognitive development have been largely limited by the accessibility to the foetus, both in imaging techniques and behavioural in paradigms. With the advent of several novel neuroimaging techniques, including *in utero* T_1/T_2 weighted and diffusion-weighted MRI (Manganaro et al., 2017) and MEG (Bisgin et al., 2021), novel structural and functional studies are likely to fill this large gap in our knowledge of early human cognitive development. Most importantly, with the higher resolution achieved in functional imaging, a linkage between the cognitive function and its neural substrate might be established; however, neuroimaging techniques and image processing protocols are highly malleable and discrepancies between different structural and functional anchors call for the establishment of a solid anchor for foetal studies, likely through the cross-validation between histological and *ex vivo* MRI studies, complemented by *in utero* structural MRI studies.

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