Indicators of fetal engagement with the environment

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Abstract

Fetal behaviour provides a non-invasive window into early fetal development, reflecting the maturation of sensory and motor systems. This thesis investigates the developmental trajectory of spontaneous and stimulus-evoked behaviours across late gestation (33–37 weeks) to identify behavioural indicators of selective sensory engagement. Secondary analyses were conducted on high-resolution ultrasound recordings using a systematic behavioural measurement framework, incorporating standardised coding of fetal behavioural states (FBS), fetal body movements (FBM), and fetal eye movements (FEM) to enhance observational reliability and analytical rigor. Quantitative analysis, including Dynamic Time Warping (DTW), was employed to distinguish baseline behavioural activity from responses elicited by controlled auditory and visual stimuli. Study 1 (N = 57) investigated patterns of FBM and FEM to determine whether observed behaviours reflected spontaneous activity or environmentally driven engagement. Results indicated that from approximately 33 weeks' gestation onward, FEM classifications increasingly aligned with behavioural markers of environmental engagement, suggesting progressive maturation of sensory–behavioural integration. Study 2 (N = 24) examined fetal behavioural responses to musical stimuli varying in timbre (string versus piano) and harmonic modality (major versus minor chords). We[1] observed distinct patterns of structured FEM and FBM across auditory conditions, indicating selective behavioural modulation in response to specific acoustic properties.

The findings from this cross-sectional study suggest that late-gestation fetuses demonstrate emerging capacities for selective engagement with environmental stimuli before birth. This research advances understanding of prenatal sensory and perceptual processing and supports refinement of fetal behavioural frameworks, with implications for clinical monitoring and foundational research into early perceptual learning.

Keywords: auditory discrimination, cross-sectional study, fetal movement, sensory engagement, ultrasound, fetal eye movements (FEM), fetal behavioural state (FBS), fetal behavioural movement (FBM)

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[1] The research for this study was conducted independently, with my supervisor and other postgraduate students involved in data collection. Consequently, “we” refers to the data collection process.

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All praise to the Almighty Allah (God) for getting me through the days when this research was torn apart, and the light seemed to be dimmed off,

ٱلْحَمْدُ لِلَّهِ رَبِّ ٱلْعَالَمِينَ

جَزَاكُمُ اللَّهُ خَيْرًا

(*Translation:* Thank you, my dear Lord, I am truly indebted to you for your mercy.)

To my beloved grandfather, whom I lost along the way this year, I hope I make you proud.

Lastly, thank you to my precious parents, Nazeer and Raeesah, for their continuous support and encouragement for raising me well to achieve my dreams – *"without your inspiration, this would not have been possible."*

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Why Study Fetal Engagement with the Environment?

Human development begins well before birth. During gestation, foundational processes supporting sensory perception, motor coordination, arousal regulation, and early learning emerge and progressively organise, providing a developmental scaffold for postnatal behaviour and cognition (Als et al., 2004; Hepper, 2015; Lecanuet & Schaal, 1996). Historically, however, the prenatal period was often treated as having limited psychological relevance, with fetal activity interpreted as predominantly reflexive or non-specific (Krasnegor et al., 1998; Joseph, 2000). Although this assumption has been substantially revised, detailed accounts of how fetuses engage with their environment, and whether such engagement reflects selective, state-modulated processing rather than generalised reactivity, remain incomplete (Lecanuet & Granier-Deferre, 2017; Piontelli, 2015; Reid & Dunn, 2021).

In this thesis, *fetal engagement with the environment* refers to stimulus-linked changes in organised behaviour that occur in addition to ongoing spontaneous activity and vary across behavioural states. Engagement is indexed using three observable markers from ultrasound: fetal behavioural state (FBS), fetal body movements (FBM), and fetal eye movements (FEM) (de Vries et al., 1982; Lecanuet et al., 2000; van Vliet et al., 1985). Because fetuses move spontaneously and cycle through sleep–wake-like states, any apparent "response" must be interpreted relative to baseline activity and state context (de Vries et al., 1985a, 1985b; Hepper, 2015).

Study 1 examines how FEM patterns relate to behavioural state under baseline conditions, and Study 2 tests whether late-gestation fetuses exhibit discriminative

behavioural modulation in response to complex auditory features, specifically timbre and harmonic modality (Armitage et al., 2025; Reid, Galati, et al., 2017; Reid & Dunn, 2021).

The developmental significance of this question is underscored by evidence that prenatal experience can shape postnatal perception and preference. Classic findings show that prenatal exposure to maternal speech can influence newborn auditory preferences, indicating continuity of learning across the birth transition (DeCasper & Spence, 1986; Moon & Fifer, 2000). More broadly, contemporary developmental accounts propose that psychological development is continuous across the prenatal and postnatal periods, and that the fetus provides a critical window for understanding the early emergence of perceptual organisation and foundational learning processes (Hepper, 2015; Lecanuet & Granier-Deferre, 2017; Reid, 2024; Reid & Dunn, 2021). Accordingly, birth is best conceptualised not as the initiation of psychological functioning, but as a developmental transition within an ongoing continuum of behavioural organisation that begins prenatally (de Vries et al., 1988; Hepper, 2015; Reid & Dunn, 2021).

Studying fetal engagement is methodologically challenging. The fetus is embedded in a complex intrauterine environment in which maternal tissue and amniotic fluid attenuate and filter sensory input while limiting direct observation (Abrams & Gerhardt, 2001; Del Giudice, 2011; Graven, 2000; Humphrey, 1978). As a result, postnatal paradigms that assume direct stimulus delivery and stable behavioural access cannot be translated directly to the prenatal context, and rapid developmental change across gestation further complicates behavioural interpretation (Hepper, 2015; Krasnegor et al., 1998). Nevertheless, advances in ultrasonography and behavioural coding frameworks increasingly permit systematic investigation of fetal behavioural organisation and its modulation by environmental stimulation (Ayala et al., 2024; Reissland & Francis, 2010).

Among sensory modalities, audition has received particular attention because sound transmission through the maternal abdomen is more reliable than that of other modalities (Abrams & Gerhardt, 2001). The key interpretive challenge is therefore not whether behaviour can be observed, but how it should be interpreted: how can observed fetal behaviour be distinguished as evidence of selective engagement rather than spontaneous activity or generalised arousal?

Addressing this question requires moving beyond binary indicators of "responsiveness" and adopting integrated behavioural frameworks that treat behavioural state, eye activity, and body movement as coordinated expressions of developing sensorimotor and regulatory systems (Lecanuet et al., 2000; Reid & Dunn, 2021; van Vliet et al., 1985). From a developmental psychology perspective, the central issue is whether fetal behaviour shows signatures consistent with arousal regulation, state-dependent sensory gating, selective processing, and early learning—constructs that are studied directly after birth but must be inferred from organised behavioural patterns in utero (Knudsen, 2007; Lecanuet & Granier-Deferre, 2017; Reid & Dunn, 2021).

Conceptual Framework of the Current Thesis

The present thesis adopts a developmental, systems-oriented framework in which fetal behaviour is conceptualised as organised activity emerging through dynamic interactions among the developing body, maturing sensory systems, and the structured constraints of the intrauterine environment (Craighero, 2024; Del Giudice, 2011; Hepper, 2015). Within this framework, FBS, FBM, and FEM are not treated as isolated outputs. Rather, they are understood as integrated expressions of developing sensorimotor organisation and regulatory control that become increasingly patterned as gestation progresses (de Vries et al., 1982; de Vries et al., 1985a, 1985b; Lecanuet et al., 2000).

Accordingly, changes in the coordination, temporal organisation, and structure of fetal behaviour are interpreted as behavioural indicators of emerging sensory readiness and state-dependent modulation, rather than as direct representations of higher-order cognition. Since direct neural measurement in utero is limited, the most defensible inferences about sensory processing come from patterns that are temporally structured, modulated by behavioural state, and distinguishable from baseline spontaneous activity (Lecanuet et al., 2000; Reid & Dunn, 2021).

A core implication of this framework is that spontaneous behaviour (SB) and stimulus-evoked behaviour (SEB) are both developmentally informative but reflect distinct underlying processes. SB primarily indexes endogenous neural self-organisation and the maturation of sensorimotor circuitry, whereas SEB provides an observable window into the developing capacity to register, filter, and selectively respond to environmental stimulation (Bekoff, 2001; Fagard et al., 2018; Lecanuet & Granier-Deferre, 2017). Clarifying how these pathways relate, and under what state conditions SEB can be interpreted reliably, motivates the thesis's emphasis on integrating FEM, FBM, and behavioural state within a unified analytic framework (Lecanuet et al., 2000; Reid & Dunn, 2021; van Vliet et al., 1985).

This conceptualisation positions the fetus as an active participant in its own developmental trajectory. Behaviour is understood not merely as reflexive output but as patterned activity that reflects the integration of sensory input, motor expression, and regulatory neural mechanisms (Craighero, 2024; Hepper, 2015; Joseph, 2000). In this way, SB and SEB are treated as complementary sources of evidence for emerging sensory selectivity, state-dependent processing, and the early foundations of learning before birth (Lecanuet & Granier-Deferre, 2017; Reid & Dunn, 2021).

Historical Foundations of Fetal Behaviour Research

Early scientific approaches to fetal behaviour were shaped by the assumption that the prenatal period was dominated by reflexive motor activity with minimal relevance for psychological development. Classical fetal observational studies documented fetal movement primarily as spinal reflexes, reinforcing a view of the fetus as neurologically immature and behaviourally passive (Hooker, 1939). In the absence of technologies capable of directly observing the fetus in utero, behavioural interpretation relied heavily on indirect indicators and postnatal inference, reinforcing uncertainty about how fetal behaviour mapped onto developing neural function (Krasnegor et al., 1998; Reissland & Francis, 2010).

The advent of real-time ultrasonography in the latter half of the twentieth century fundamentally altered this perspective. Groundbreaking ultrasound studies by Birnholtz (1981) demonstrated that fetal movements are neither random nor purely reflexive but can show logical organisation and developmental progression across gestation (Birnholtz, 1981; de Vries et al., 1985a, 1985b). These observations provided the first empirical basis for interpreting fetal behaviour as an index of psychological perception and a function of central nervous system (CNS) maturation rather than peripheral motor output alone (Einspieler et al., 2004; Lecanuet et al., 2000; Piontelli, 2015).

Although foundational, early ultrasound studies were limited by low temporal resolution and crude behavioural categorisation. Sensory responsiveness was often inferred from gross motor reactions or changes in heart rate, reinforcing a binary, detection-based model of sensory processing (Krasnegor et al., 1998; Lecanuet et al., 2000; Moser & Visser, 2009). These limitations motivated later methodological

refinement and increasing emphasis on baseline-referenced, state-sensitive interpretation (Ayala et al., 2024; Reissland & Francis, 2010; Reid & Dunn, 2021).

Fetal Behaviour and Early Behavioural Organisation

Human development is a continuous, experience-dependent process that begins well before birth and unfolds throughout gestation through the progressive differentiation and integration of neural systems (Stiles & Jernigan, 2010). During the prenatal period, fetuses display an increasingly structured repertoire of behaviours that reflect CNS maturation and the psychological emergence of sensory, motor, and regulatory capacities (de Vries et al., 1985a, 1985b; Hepper, 2015; Piontelli, 2015). Even before external stimulation, the developing nervous system is intrinsically active (Bekoff, 2001; Fagard et al., 2018).

Even before external stimulation, the developing nervous system is intrinsically active (Fagard et al., 2018; Hepper, 2015). Spontaneous fetal movements, self-initiated motor patterns occurring without identifiable external triggers, are widely recognised as behavioural markers of neurodevelopmental integrity and early fetal sensorimotor network formation (D'Elia et al., 2001; de Vries et al., 1985a, 1985b; Hadders-Algra, 2018).

During gestation, spontaneous movement patterns change systematically in quality, complexity, and coordination, reflecting maturation of neuromuscular pathways and central regulatory mechanisms (D'Elia et al., 2001; Hadders-Algra, 2018; Marschik et al., 2007). These movements are generated by the early organisation and spontaneous firing of neural circuits within the developing CNS, rather than by reflexive responses to environmental events (de Vries et al., 1982; Lecanuet et al., 2000; van Vliet et al., 1985). This developmental baseline is essential for interpretation, because any claim of stimulus-

linked engagement must be evaluated against ongoing spontaneous behavioural organisation (de Vries et al., 1982; Lecanuet et al., 2000; van Vliet et al., 1985).

Ultrasound-Based Observation of Fetal Behaviour

Real-time ultrasonography enables continuous, non-invasive observation of fetal movement patterns, eye activity, and behavioural organisation across gestation (Birnholtz, 1981; Hoffman et al., 1986; Reissland & Francis, 2010). Importantly, ultrasound observation supports analysis of timing, coordination, and behavioural context, allowing researchers to examine behavioural organisation rather than relying on isolated reactions. Modern approaches increasingly emphasise baseline-referenced interpretation and explicit modelling of behavioural state, because fetal activity and the coupling among behavioural channels vary systematically across gestation and states (Ayala et al., 2024; Lecanuet et al., 2000; Reid & Dunn, 2021). This methodological foundation is central to the present thesis: to infer engagement with environmental stimuli, behavioural changes must be interpreted relative to baseline spontaneous organisation and within behavioural state context, rather than treated as isolated "responses" (Lecanuet et al., 2000; Reid & Dunn, 2021).

Development of Fetal Sensory Systems and the Intrauterine Environment

Fetal sensory systems develop hierarchically and modality-specifically, progressively enabling detection of and responsiveness to features of the intrauterine environment (Hepper, 2015; Lecanuet & Schaal, 1996; Querleu et al., 1988). Sensory maturation does not occur in isolation; it unfolds in continuous interaction with spontaneous motor activity, behavioural state organisation, and the physical constraints of the uterus (Craighero, 2024; Del Giudice, 2011). Consequently, the developmental timing of sensory system maturation constrains when stimulus-evoked engagement can be expected

and how behavioural responses should be interpreted (Lecanuet & Granier-Deferre, 2017; Reid & Dunn, 2021).

Auditory responsiveness becomes reliably observable during the second and third trimesters, reflecting maturation of peripheral auditory structures and central pathways that support sensory processing and regulation (Elliott et al., 1995; Kisilevsky et al., 2000; Querleu et al., 1988). The intrauterine auditory environment is acoustically constrained: external sounds are attenuated and spectrally filtered by maternal tissue and amniotic fluid, reducing higher-frequency components while preferentially preserving lower-frequency, rhythmic, and prosodic information (Abrams & Gerhardt, 2001; Graven, 2000).

As a result, the fetus is consistently exposed to a structured soundscape dominated by maternal physiological rhythms and a filtered but prosodically rich version of the maternal voice (Graven, 2000; Moon & Fifer, 2000). Evidence indicates that fetuses are sensitive to salient acoustic features such as rhythm and prosodic contour, suggesting that meaningful information is preserved despite intrauterine filtering and may support early learning-related processes (DeCasper & Spence, 1986; Hepper, 1991; Kisilevsky et al., 2004; Lecanuet & Granier-Deferre, 2017).

In comparison, visual experience in utero is more constrained, with opportunities for patterned stimulation depending on environmental conditions and attenuation through maternal tissue, complicating strong claims about fetal visual “attention” in the postnatal sense (Del Giudice, 2011). Nonetheless, ultrasound studies have reported fetal eye movements and behavioural modulation in response to visual stimulation, suggesting that late gestation may support rudimentary forms of visually driven orienting under appropriate conditions (Donovan et al., 2020; Donovan, Reissland, & Reid, 2020). In the

present thesis, visual findings are treated as convergent evidence that state-linked modulation can be observed in fetal oculomotor behaviour, rather than as direct evidence of mature attentional processes.

Collectively, these sensory development trajectories suggest that late gestation is a critical window when sensory systems are sufficiently mature for environmental input to modulate behavioural organisation, while regulatory and motor systems remain in rapid transition (Hadders-Algra, 2018; Hepper, 2015; Lecanuet & Granier-Deferre, 2017). The present thesis therefore focuses on late gestation (33–37 weeks) to examine whether behavioural modulation to controlled stimulation can be distinguished from baseline spontaneous activity, consistent with evidence that behavioural states systematically gate responsiveness and organise stimulus-linked behaviour (de Vries et al., 1982; van Vliet et al., 1985; Van Heteren et al., 2001a).

Auditory Discrimination and Musical Processing in Utero

The fetal auditory system undergoes substantial maturation during the second and third trimesters, enabling detection of structured acoustic input by approximately 25–28 weeks' gestation (Elliott et al., 1995; Kisilevsky et al., 2000; Querleu et al., 1988). Because stimuli are transmitted through the maternal abdomen in a spectrally filtered form that preserves low-frequency and rhythmic/prosodic information, behavioural differentiation of acoustic features implies more complex processing than detection alone (Abrams & Gerhardt, 2001; Lecanuet & Granier-Deferre, 2017).

Neurophysiological evidence indicates that the fetal brain can show stimulus-locked auditory responses during late gestation. Fetal magnetoencephalography research demonstrates developmental changes in fetal auditory evoked fields consistent with maturation of auditory pathways and cortical responsiveness (Holst et al., 2005; Niepel et al.,

2020; Siegel et al., 2021). Importantly, reports of fetal discrimination of structured auditory regularities support the interpretation that late-gestation auditory processing can extend beyond non-specific reactivity, although such findings require careful interpretation in light of behavioural state and baseline organisation (Holst et al., 2005; Niepel et al., 2020; Reid, Croci, et al., 2020).

Complementing these neural findings, behavioural work provides evidence for prenatal auditory learning. Newborn preferences for prenatally experienced speech stimuli and demonstrations of transnatal auditory learning indicate that prenatal exposure can shape postnatal recognition and preference (DeCasper & Spence, 1986; Moon & Fifer, 2000). Reviews of fetal perception and memory further argue that late gestation supports experience-dependent encoding under appropriate stimulus conditions, consistent with continuity models of early learning across birth (Lecanuet & Granier-Deferre, 2017; Mann & Fuchs, 2022).

However, much prenatal auditory research focuses on relatively simple contrasts, such as intensity, rhythm, or voice familiarity. Far less is known about fetal sensitivity to complex musical attributes, including timbre and harmonic modality. In postnatal listeners, these attributes contribute to perceptual categorisation and reliable affective interpretation, and their processing is supported by hierarchical organisation in auditory cortex (Armitage et al., 2025; Bonetti & Costa, 2019; Humphries et al., 2010; Norman-Haignere et al., 2021). These findings provide a principled basis for examining whether fetuses exhibit differentiated engagement with higher-order acoustic features prior to birth, while recognising that fetal behavioural evidence reflects early developmental precursors of selective processing rather than mature musical cognition (Reid & Dunn, 2021).

Establishing such discrimination in utero requires designs that separate stimulus-linked change from spontaneous variability and state-dependent motor availability, given that

fetal behaviour is strongly organised by intrinsic state fluctuations and endogenous activity (de Vries et al., 1982; Lecanuet et al., 2000; van Vliet et al., 1985).

Behavioural Indicators of Fetal Engagement

Behavioural indicators are the primary means of assessing fetal sensory engagement in utero. Among these, behavioural state, eye movements, and body movements are central markers of developing sensorimotor integration and regulatory maturation (de Vries et al., 1982; Lecanuet et al., 2000; van Vliet et al., 1985). As gestation progresses, fetal behaviour becomes increasingly organised into behavioural states that resemble patterned sleep–wake-like cycles, reflecting varying levels of arousal and central organisation (Arduini et al., 1995; de Vries et al., 1982; Hunter et al., 1982). These states are identified through coordinated indices such as heart rate patterning, presence or absence of eye movements, and movement quantity and quality (van Vliet et al., 1985; Lecanuet et al., 2000). For this reason, the present thesis focuses on integrated behavioural markers and baseline-controlled analyses in late gestation to support more specific inferences about engagement (Lecanuet et al., 2000; Reid & Dunn, 2021).

Fetal body movements are widely used indicators of central nervous system maturation. Longitudinal and qualitative studies show systematic changes in movement frequency, complexity, and coordination across gestation, reflecting progressive neuromuscular and central regulatory development (D'Elia et al., 2001; de Vries et al., 1985a, 1985b; Hadders-Algra, 2018; Marschik et al., 2007). Although body movements can be sensitive to external stimulation, interpretive specificity is limited unless behaviour is evaluated relative to baseline spontaneous organisation and within the behavioural state context (Lecanuet et al., 2000; Moser & Visser, 2009; Van Heteren et al., 2001a).

In contrast, fetal eye movements are more tightly coupled to behavioural state regulation and the emerging neural organisation. Within classical behavioural state frameworks, oculomotor activity was treated as a defining marker of sleep–wake cycling, with fetal eye movement patterns distinguishing states and reflecting central nervous system maturation (Birnholtz, 1981; van Vliet et al., 1985). This functional embedding suggests that FEM are not merely peripheral motor events but rather behavioural expressions of coordinated brainstem and central processes that support arousal regulation and gating. Accordingly, FEM may offer a more direct window into sensory readiness and state-linked modulation. Eye movements are closely tied to arousal regulation, sleep–wake cycling, and coordinated neural activity, positioning them as potential indicators of selective engagement rather than generalised motor output (Arnulf, 2011; Birnholtz, 1981; Donovan et al., 2020; van Vliet et al., 1985).

FEM patterns also vary systematically with gestational age and behavioural state, reflecting the progressive maturation of oculomotor control and central state organization (Birnholtz, 1981; Hoffman et al., 1986; de Vries et al., 1982; van Vliet et al., 1985). Within this thesis, FEM are therefore treated as indices of state-dependent sensory readiness and early modulation, particularly when interpreted alongside behavioural state and concurrent body movement (Lecanuet et al., 2000; Reid & Dunn, 2021).

Behavioural state provides essential context for interpreting both body and eye movements. Because state modulates sensory gating and motor expression, identical stimuli may elicit different behavioural patterns depending on the fetus's prevailing state (Van Heteren et al., 2001a; van Vliet et al., 1985). Without explicit state modeling, behavioural differences can be misattributed to discrimination when they instead reflect state-driven variability in gating or motor availability (Lecanuet et al., 2000; Van Heteren

et al., 2001a). For this reason, behavioural state is treated in this thesis as a necessary interpretive condition for evaluating stimulus-evoked behaviour and for differentiating selective engagement from non-specific reactivity (Reid & Dunn, 2021).

Within the classical FBS framework, four behavioural states, 1F to 4F, are distinguished, broadly corresponding to quiet sleep, active sleep, transitional states, and quiet awake periods (Table 1). These states become increasingly stable during late gestation, reflecting maturation of central regulatory mechanisms (Nijhuis et al., 1982; Piontelli, 2015).

Table 1

Description of Fetal Behavioural States (1F–4F)

Fetal Behavioural State	Description
State 1F – Quiet Sleep	Characterised by minimal or absent body movement, absence of FEM, and a stable, regular heart rate pattern.
State 2F – Active Sleep	Defined by frequent body movements and the presence of FEM, while heart rate remains stable and shows normal variability.
State 3F – Transitional	A relatively rare state marked by features intermediate between 2F and 4F, often short in duration and less clearly defined.
State 4F – Quiet Awake	Characterised by sustained high activity levels, continuous eye movements, and an unstable or more variable heart rate pattern.

Critically, sensory responsiveness is strongly modulated by FBS. Auditory and visual responses are more likely to occur during active or aroused states, such as 2F and 4F, than during quiet sleep, 1F, highlighting the need to contextualise behavioural change within the prevailing arousal organisation (de Vries et al., 1985; Van Heteren et al., 2001; Niepel et al., 2020; van Vliet et al., 1985). Without explicit state control, behavioural differences may be

misattributed to discrimination when they instead reflect state-driven variability in sensory gating or motor availability (Lecanuet et al., 2000). For this reason, FBS is treated in this thesis as a necessary interpretive condition for evaluating stimulus-evoked behaviour and for differentiating selective engagement from non-specific reactivity.

Fetal Behavioural States and State-Dependent Sensory Processing

Habituation paradigms have frequently been used to infer fetal learning and early attentional readiness, with reduced responsiveness to repeated stimulation followed by recovery to novel input interpreted as evidence of memory and discrimination (Groome et al., 1993; Hepper & Shahidullah, 1992; Leader et al., 1982; Van Heteren et al., 2001a). However, interpretation is complicated by concurrent developmental changes in behavioural state, arousal regulation, and spontaneous motor activity, each of which can influence responsiveness independently of stimulus properties (de Vries et al., 1982; Lecanuet et al., 2000).

Evidence that habituation and dishabituation vary across gestational age and differ by fetal state further underscores the importance of explicit state modelling in fetal learning paradigms (McCorry & Hepper, 2007; Sandman et al., 1997; Van Heteren et al., 2001a). These considerations align with broader developmental psychology accounts in which attention and learning are fundamentally state-dependent, emerging through the interaction of arousal systems and sensory processing constraints (Knudsen, 2007; Reid & Dunn, 2021).

Modern Approaches to Fetal Behavioural Measurement

Contemporary fetal behavioural research has benefited from advances in imaging, analytical methods, and behavioural coding. Two-dimensional (2D) and four-dimensional (4D) ultrasonography now enable increasingly continuous, high-resolution observation of fetal movements, facial activity, eye movements, and state transitions, enabling researchers to

quantify behavioural organisation rather than relying on global impressions. For example, fine-grained 4D facial coding shows clear developmental increases in coordinated action patterns: between 24 and 35 weeks' gestation, the mean proportion of co-occurrences of three or more facial movements increased from 7% to 69%, alongside increases in "cry-face gestalt" co-occurrences from 0% to 42% and "laughter-face gestalt" co-occurrences from 0% to 35% (Reissland et al., 2011).

These coordinated changes align with the core assumption of the present thesis that late-gestation behaviour is meaningfully structured and best interpreted as multicomponent organisation (e.g., FEM–movement coordination and state-linked patterning) rather than as isolated reflex output. More broadly, modern fetal behavioral frameworks emphasise baseline-referenced interpretation and state dependence, because fetal activity, reactivity, and coupling among systems (e.g., motor activity with autonomic indices) change systematically across gestation and vary by behavioural state (DiPietro, 1996; DiPietro et al., 2015).

Crucially, contemporary stimulus studies also show that response magnitude and form depend on both baseline and state, supporting this thesis's SB–SEB distinction. In a large 2D ultrasound reanalysis using a structured before/during/after design (94 scans), light presentation increased both head and eye movements, with mean eye movements rising from 0.2 ($SE = 0.05$) before stimulation to 0.7 ($SE = 0.12$) during stimulation and remaining elevated at 0.6 ($SE = 0.08$) afterward; these changes were statistically reliable (e.g., during vs. before, $Z = -3.716$, $p < .001$; after vs. before, $Z = -4.155$, $p < .001$) (Donovan, 2020).

This pattern is consistent with the thesis's claim that fetal behaviour during stimulation should be evaluated relative to baseline state organisation, because elevated post-stimulus responding can reflect sustained oculomotor control or arousal-related carryover rather than "random movement." Relatedly, Donovan (2020) summarises earlier state-contingent findings

in which positive response rates to light were high (82%) when fetuses were in active sleep or quiet awake, illustrating how apparent "non-response" can reflect state-related gating rather than absent sensory processing. This context underscores the need for standardised, state-sensitive frameworks capable of differentiating spontaneous behaviour from stimulus-linked modulation (Reid & Dunn, 2021).

Nevertheless, methodological heterogeneity remains a central challenge, limiting comparability and contributing to mixed conclusions about fetal sensory processing. Recent studies argue that 4D ultrasound has not "revolutionised" fetal movement science largely because studies diverge in sampling windows, frame/volume rates, stimulus parameters, operational definitions of movement classes, and reliability practices, which collectively undermine cross-study synthesis (Pretti et al., 2022). This concern is echoed in broader reviews of prenatal sound stimulation, which repeatedly note wide variation in stimulus type (music vs. speech), intensity and safety reporting, exposure timing, and outcome definitions, making it difficult to map consistent dose–response relations across studies (Movalled et al., 2023).

Against this backdrop, the present thesis directly addresses the comparability problem by using baseline-controlled analyses, explicitly operationalising FEM/SB/SEB within a structured ethogram, and adopting a state-sensitive interpretation (Lecanuet et al., 2000; Reid & Dunn, 2021). This approach is conceptually aligned with contemporary fetal behavioural emphases while targeting the specific sources of heterogeneity that have impeded cumulative inference in the fetal engagement literature.

Methodological Imperatives

FEM have long been used as indices of behavioural state and neurological maturation, with early observational frameworks proposing discrete FEM patterns as markers of sleep–wake cycling and central nervous system development (Birnholtz, 1981; Nijhuis et al., 1982).

These classical schemes were foundational in demonstrating that fetal behaviour is organised rather than random, linking patterned oculomotor activity with emerging behavioural states and providing some of the earliest evidence of prenatal behavioural regulation (Pretti et al., 2022). However, advances in high-resolution ultrasonography have revealed important limitations in the validity, reproducibility, and interpretive precision of these early classifications (Birnholtz, 1981). Contemporary reviews indicate that classical FEM categories are often inconsistently defined, variably applied across laboratories, and subject to substantial inter-rater disagreement, thereby reducing their reliability as developmental or state markers (Reissland & Francis, 2010).

These concerns are particularly consequential when interpreting stimulus-evoked behaviour, because inaccurate or overly broad FEM categorisation can obscure whether observed eye activity reflects endogenous state organisation or genuine stimulus-linked modulation. Without clear operational definitions and state validation, increased eye movements during stimulation may be misattributed to perceptual responsiveness when they instead reflect spontaneous fluctuations in arousal or behavioural state. As DiPietro and colleagues argue, fetal behaviour must be interpreted relative to baseline organisation and concurrent state, since motor expression, autonomic activity, and sensory responsiveness are tightly coupled and vary systematically across states (DiPietro, 1996; DiPietro et al., 2015). Consequently, behavioural context is not ancillary but central to valid inference.

Several additional methodological constraints further complicate the interpretation of fetal behaviour. First, many studies do not clearly distinguish spontaneous from stimulus-evoked activity, increasing the likelihood that endogenous movements are misclassified as responses to experimental manipulation. Second, behavioural state is frequently inferred indirectly or omitted from analysis altogether, despite evidence that state modulates sensory

gating, motor threshold, and responsivity. Nijhuis et al. (1982) demonstrated that FBS differ markedly in motor activity and physiological organisation. However, later stimulus studies often collapse across these states, thereby conflating state-dependent variability with stimulus effects. Third, some classical FEM categories lack clear anatomical or physiological grounding. For instance, the historically defined "Type III" category has been described inconsistently and is poorly specified, limiting reproducibility and developmental interpretability, a problem explicitly noted in modern ultrasound validation work (Woitek et al., 2013).

Recent technological and analytical advances suggest that more objective, state-sensitive frameworks are achievable. High-resolution imaging now enables fine-grained temporal tracking of eye-body coordination, and emerging computational approaches, including automated motion tracking and machine-learning classification, have the potential to reduce subjective coding bias and enhance reproducibility (Vasung et al., 2023). Nevertheless, these approaches remain underutilised in research specifically examining fetal sensory engagement. Much of the field continues to rely on outdated, unprocessed coding schemes developed before the advent of modern imaging capabilities. Accordingly, the present thesis adopts a refined behavioural coding strategy that integrates explicit FEM definitions with concurrent behavioural state validation and baseline-controlled analyses, thereby strengthening the interpretive separation between spontaneous behaviour and potential stimulus-evoked modulation.

Research Gap

Although substantial evidence indicates that fetuses detect and respond to sensory input, conceptualisation and measurement of fetal engagement remain limited. Many studies operationalise responsiveness using binary indicators, such as the presence of movement or

changes in heart rate. While these approaches can establish detection, they provide limited insight into behavioural organisation, selectivity, or coordination and therefore cannot adequately test whether fetal behaviour reflects discriminative processing or non-specific arousal (Krasnegor et al., 1998; Lecanuet et al., 2000; Moser & Visser, 2009).

Behavioural state is also often under-integrated in stimulus research, despite repeated evidence that variability in responsiveness frequently reflects differences in baseline state rather than differences in sensory processing per se (Van Heteren et al., 2001a; van Vliet et al., 1985). Similarly, FEM classifications have rarely been systematically embedded within comprehensive behavioural-state frameworks aligned with modern imaging standards, constraining their usefulness as indices of engagement (Ayala et al., 2024; Reissland & Francis, 2010).

Finally, while basic auditory responsiveness and learning are well documented, fetal discrimination of complex acoustic properties remains underexamined. Reviews of prenatal auditory stimulation note variability in stimulus type and outcome definitions, and systematic reviews highlight the need for clearer mechanistic interpretation and stronger designs (Ko & Shim, 2020; Sani et al., 2023).

In contrast, postnatal research shows that timbre and harmonic modality contribute to perceptual categorisation and affective interpretation and are supported by hierarchical auditory cortical organisation (Armitage et al., 2025; Humphries et al., 2010; Norman-Haignere et al., 2021). Establishing differentiated behavioural modulation to such features in utero would therefore be developmentally meaningful, but requires baseline-controlled, state-sensitive designs to separate stimulus-linked change from spontaneous variability (Lecanuet & Granier-Deferre, 2017; Reid & Dunn, 2021).

In response to these conceptual and methodological limitations, this thesis advances an integrated, state-sensitive framework for investigating fetal engagement during late gestation, a developmental window characterised by rapid maturation of sensory–motor integration and behavioural state organisation (de Vries et al., 1982; Hepper, 2015; Lecanuet & Granier-Deferre, 2017). Across two complementary studies, the thesis distinguishes spontaneous behaviour from potential stimulus-evoked modulation through baseline-controlled comparisons, integrates refined FEM coding with behavioural state validation, and tests discriminative behavioural modulation to complex auditory features, specifically timbre and harmonic modality (Armitage et al., 2025; Lecanuet et al., 2000; Reid & Dunn, 2021).

Research Questions and Hypotheses

Guided by this framework, the thesis examines whether late-gestation fetal behaviour provides evidence of organised, state-dependent sensory engagement and whether such engagement varies with gestational age and stimulus characteristics. First, it evaluates whether FEM patterns systematically covary with behavioural state under baseline conditions, consistent with endogenous oculomotor organisation (RQ1) (Birnholtz, 1981; de Vries et al., 1982; van Vliet et al., 1985).

Second, it assesses developmental change in behavioural coordination across 33-37 weeks' gestation (RQ2), consistent with evidence of increasing organisation and stability of state-linked behavioural patterns in late gestation (de Vries et al., 1985a; Hadders-Algra, 2018; van Vliet et al., 1985).

Third, it tests whether fetuses exhibit discriminative modulation to complex auditory stimuli, including differences between musical timbres and harmonic modalities (RQ3), grounded in evidence that fetuses are sensitive to properties of speech and music and that

prenatal auditory learning supports transnatal continuity (DeCasper & Spence, 1986; Kisilevsky et al., 2004; Moon & Fifer, 2000; Reid, Galati, et al., 2017).

It is hypothesised that the frequencies of distinct FEM types will be significantly associated with defined behavioural states under baseline conditions, reflecting state-modulated oculomotor organisation (H1, RQ1) (Birnholtz, 1981; van Vliet et al., 1985). It is predicted that fetuses will show higher behavioural response frequencies to string timbre than to piano timbre and to minor chords than to major chords, consistent with discriminative processing rather than non-specific arousal (H2, RQ3), informed by evidence that fetuses can show sensitivity to acoustic properties of speech and music and that timbre and modality are perceptually meaningful features in later development (Armitage et al., 2025; Reid, Galati, et al., 2017). Finally, it is hypothesised that stimulus-linked responsiveness increases from 33 to 37 weeks of gestation, consistent with the progressive maturation of sensory–motor integration and state-dependent modulation (H3, RQ2) (de Vries et al., 1985a; Hadders-Algra, 2018; Lecanuet et al., 2000).

Together, these questions and hypotheses provide a structured basis for determining whether late-gestation fetal behaviour reflects baseline-referenced, state-modulated sensory engagement and discriminative behavioural responses to complex environmental information before birth (Lecanuet & Granier-Deferre, 2017; Reid & Dunn, 2021).

Methods

Overview and Methodological Rationale

Given the ethical and practical constraints on direct neural measurement in utero, this research adopts a behavioural observational approach, using secondary analysis of high-resolution ultrasound recordings. Behavioural markers, including FBS, FBM, and FEM, were

coded using a structured ethogram and analysed under baseline-controlled and state-validated conditions.

This thesis aims to determine whether fetal behavioural patterns in late gestation reflect state-dependent selective sensory engagement, rather than non-specific reactivity, and whether such engagement varies across gestational age and auditory stimulus properties. The methodology was designed to operationalise the three research questions and associated hypotheses directly. This approach enables differentiation between SB and SEB, which is central to evaluating selective sensory engagement.

Design

Two interconnected studies were conducted. Study 1 examined baseline behavioural organisation and associations between FEM and FBS to test state-dependence (RQ1; H1). Study 2 examined whether fetuses demonstrate discriminative behavioural responses to complex auditory stimuli varying in timbre and harmonic modality (RQ3; H2), while also allowing assessment of developmental change across gestational age (RQ2; H3).

This research employed a cross-sectional observational design with secondary analysis of ultrasound data collected during late gestation (33–37 weeks). This developmental window was selected because it is characterised by the rapid maturation of sensorimotor integration and increasingly stable organisation of behavioural states.

Both studies further integrated a within-subjects design, comparing fetal behaviour during baseline periods of undisturbed activity with behaviour during experimentally defined stimulus periods. This approach reduced inter-individual variability by anchoring interpretation to each fetus's own spontaneous behavioural profile and enabled evaluation of stimulus-linked behavioural modulation within participants. Study 1 focused on baseline state-related

organisation of ocular behaviour, whereas Study 2 examined behavioural responses to acoustically complex stimulation under comparable conditions.

Participants and Data Sources

Study 1

The dataset was derived from high-resolution ultrasound scans collected during routine prenatal monitoring sessions, within which research stimulus protocols were embedded. Inclusion criteria were established to ensure participant safety and to preserve stimulus integrity. Eligible cases involved singleton pregnancies with no known obstetric complications or maternal medical conditions likely to influence fetal behavioural state or wellbeing, and a maternal body mass index (BMI) ≤ 30 at the start of pregnancy.

Study 1 initially comprised 100 ultrasound recordings obtained from 76 pregnant participants, with some participants contributing more than one recording. Recordings were acquired between 231 and 252 days' gestation, corresponding to 33 to 36 weeks, with a mean gestational age of 241.55 days (SD = 6.06).

To optimise the likelihood that the visual stimulus reached the fetus, maternal tissue thickness was assessed for all recordings. Thickness was measured from the skin surface to the anterior uterine wall and ranged from 13 to 60 mm (M = 33.2, SD = 11.1). A threshold of 60 mm was applied as an exclusion criterion because attenuation beyond this value reduces light transmission, compromising stimulus consistency and the interpretability of fetal visual responsiveness.

Exclusions occurred across multiple stages. First, 19 recordings were excluded following initial screening: 13 due to poor scan quality (e.g., corrupted files or insufficient resolution), five due to fetal positioning that obscured key anatomical landmarks required for

reliable ocular tracking, and one due to maternal tissue thickness exceeding the 60 mm threshold. Following recording-level exclusions, additional cases were removed at the participant level where no remaining recordings met analytic requirements.

The final analytic sample for Study 1 comprised 57 clinically healthy pregnant participants, each contributing one eligible recording to the analysis. Demographic variables were not available for the present analyses. The dataset comprised retrospectively obtained, de-identified ultrasound recordings, and no participant-level sociodemographic information was accessible to the research team.

Study 2

Participants were recruited through the University of Waikato Infant Research Group and the Women's Health Clinic. Eligibility criteria were consistent with Study 1 (singleton pregnancy; absence of major pregnancy complications likely to influence fetal behavioural state or wellbeing; capacity to understand study instructions). Study 2 comprised 23 pregnant participants between 245 and 252 days' gestation (35–37 weeks; M = 248.9 days, SD = 2.4). Prior to participation, a qualified diagnostic medical sonographer verified normal fetal development via ultrasound examination.

Demographic information was collected via a structured questionnaire. It included maternal age, self-identified ethnicity, obstetric history, and contextual variables relevant to prenatal auditory exposure, including habitual music listening, exposure to loud environmental noise, and substance use. Although demographic data were limited, the Study 2 sample reflected the ethnic diversity of the Waikato region, comprising participants identifying as New Zealand European, Māori, Pacific Peoples, and Asian.

Ultrasound Recording Procedures

All ultrasound recordings were acquired using high-resolution two-dimensional (2D) ultrasound systems capable of capturing continuous fetal movement and detailed ocular activity. Recordings were obtained using a Philips Epiq 7 ultrasound system in dedicated sonography rooms at Waikato Hospital and lasted approximately 45–60 minutes. To maximise image stability and minimise motion artefact, participants were positioned in a semi-recumbent posture throughout data acquisition, and standard biometric checks were completed prior to experimental procedures to confirm maternal and fetal well-being.

Each recording session comprised two systematically defined phases: baseline periods, during which no controlled sensory stimulation was administered, and stimulus periods, during which auditory or visual stimuli were presented in a controlled, time-locked manner. The inclusion of baseline recordings was methodologically essential for establishing each fetus's spontaneous behavioural profile, providing a critical reference framework for differentiating spontaneous behaviour from stimulus-evoked behaviour, in line with the objectives of RQ1.

Across both studies, stimulus presentation was time-locked to ultrasound acquisition and annotated using digital timestamps or on-screen markers to enable precise alignment between behavioural coding and stimulus events. Ultrasound recordings were coded using specialised behavioural observation software, enabling frame-by-frame analysis of fetal eye movements, behavioural state, and body movements. Coders received extensive training in identifying ocular landmarks and movement trajectories, and a subset of recordings was independently double-coded to assess reliability; discrepancies were resolved through discussion and consensus. This approach aligns with established standards in fetal behavioural research and supports the reliability of the resulting dataset (DiPietro et al., 2015; Reid & Dunn, 2021).

Participants were instructed to remain silent and still during scanning to minimise artefacts arising from maternal movement or voice vibration. In cases where fetal inactivity limited behavioural observability, participants were occasionally asked to walk briefly and return for rescanning to increase the likelihood of capturing active behavioural states.

Experimental Stimuli

Auditory Stimuli

Study 1 (Pure tone)

In Study 1, the auditory stimulus was a 500 Hz pure tone presented at 90 dB SPL from a calibrated external speaker positioned approximately one metre from the maternal abdomen. The tone was delivered as a 2-second beep every 6 seconds. Exposure parameters adhered to prenatal auditory safety recommendations (Committee on Environmental Health, 1997; Graven, 2000).

Study 2 (Timbre and harmony)

In Study 2, two structured auditory paradigms were designed to assess fetal discriminative behavioural responses to higher-order acoustic features under controlled conditions. The first paradigm targeted timbre discrimination by presenting an identical musical note across different instrumental sources while holding pitch, duration, and amplitude constant, thereby isolating variation in spectral envelope as the primary acoustic dimension. The second paradigm examined harmonic modality discrimination by contrasting major and minor chords that differed principally in the intervallic structure of the third (e.g., C–E–G versus C–E♭–G), allowing sensitivity to harmonic organisation to be assessed while minimising confounding differences in fundamental frequency and temporal properties.

Stimuli were delivered via a calibrated external loudspeaker positioned over the estimated location of the fetal head. Sound intensity was adjusted based on maternal tissue thickness to ensure consistent intrauterine exposure and to remain within established safety limits (Graven, 2000). To reduce maternal auditory interference and attentional distraction, participants wore over-ear earmuffs during stimulus presentation. Selection of these stimulus dimensions was theoretically informed by postnatal evidence demonstrating that timbre and harmonic modality support perceptual discrimination and affective processing, and by the absence of prior fetal research systematically examining these acoustic contrasts within a state-controlled behavioural framework.

Visual Stimuli

Where visual stimulation was present, light stimuli were delivered externally and filtered through maternal tissues. Visual data were analysed only when fetal ocular visibility met coding criteria. Visual stimuli were included to support broader assessment of sensory engagement (RQ1) but were not the primary focus of discrimination analyses. In Study 1, visual stimulation was delivered using a 4 mm red LED (650 nm), selected to optimise transabdominal transmission while remaining within established safety parameters. Light intensity was calibrated relative to maternal tissue thickness to standardise luminance reaching the fetus: 0.5 mW (≤ 15 mm), 1 mW (15–30 mm), and 5 mW (≥ 30 mm). During presentation, the light source was moved continuously across the periphery of the fetal face to elicit orienting or avoidance eye movements and to reduce the likelihood that observed ocular activity reflected spontaneous scanning alone.

Behavioural Coding Framework

Ultrasound recordings were coded using *The Observer XT* version 16 (Noldus Information Technology), which enabled continuous visualisation and event-level annotation

of fetal movement and ocular activity. Coding was conducted on de-identified recordings, with audio muted to maintain partial blinding to experimental condition and to minimise expectancy effects. Each session was segmented into predefined baseline and stimulus blocks using embedded digital timestamps and on-screen markers to ensure precise temporal alignment between behavioural events and stimulus presentation. Prior to formal coding, coders reviewed approximately 30 seconds of baseline footage to familiarise themselves with fetal orientation and to identify relevant anatomical landmarks for accurate ocular and movement classification. Breathing movements were not coded, as they were not interpretable as indices of sensory engagement within the present behavioural framework.

Coding of FBS

FBS was coded as a higher-order organisational variable, derived from the integrated patterning of FBM and FEM, which were coded independently as primary behavioural measures. FBS coding was undertaken concurrently with behavioural annotation to provide a state-based interpretive context for evaluating stimulus-linked behavioural change, rather than as a direct measure of motor output.

State classification followed established FBS frameworks (Nijhuis et al., 1982) and was informed by the relative presence or absence and temporal organisation of FBM and FEM across sustained observation windows. Importantly, individual FBM or FEM events were not used in isolation to assign a state. Instead, FBS was inferred from the overall coordination, continuity, and stability of these behaviours, consistent with the conceptualisation of behavioural state as an emergent property of fetal behavioural organisation.

Patterns of FBM activity, including periods of motor quiescence, intermittent movement, or sustained and variable motor output, were used to index overall behavioural activation. FEM information, where ocular structures were visible, was used to refine state

classification by indicating levels of central activation and behavioural organisation. Concordant patterns of low FBM and absent FEM were indicative of quiet behavioural states, whereas increased FBM accompanied by intermittent or sustained FEM informed classification of active or transitional states. When FEM visibility was limited due to fetal position or imaging constraints, state classification relied primarily on the organisation of FBM patterns, and such segments were conservatively coded to minimise misclassification.

FBS coding was applied across both baseline and stimulation epochs to distinguish stimulus-linked behavioural modulation from state-dependent variability in spontaneous activity. This approach directly addressed RQ1, which concerns whether fetal engagement with sensory stimulation varies with behavioural state. FBS was treated analytically as a contextual control variable, enabling interpretation of FBM and FEM responses relative to the prevailing state rather than assuming behavioural equivalence across conditions. Heart rate and other autonomic measures were not available in either study, and behavioural state determination therefore relied exclusively on the integrated organisation of FBM and FEM, consistent with ultrasound-based fetal research in which physiological indices are unavailable.

Coding of FBM

FBM included general movements, startles, isolated limb movements, and directed actions such as hand-to-face or hand-to-mouth contact. FBM were coded FEM and FBS independently and constituted the primary motor behavioural measure used to quantify spontaneous and stimulus-linked activity. Coding was conducted during both baseline and stimulus periods to enable evaluation of stimulus-related modulation relative to each fetus's spontaneous motor profile. In Study 2, FBM were coded frame-by-frame using a modified behavioural ethogram adapted from de Vries et al. (1982) (see Table 2). Continuous video recordings were reviewed at standard playback speed with frame-by-frame verification where

required to determine precise movement boundaries. Each behavioural event was annotated with onset and offset frames, permitting calculation of both frequency (number of events) and duration (total time active) spectral envelope variation within each observation epoch. Coding across entire recording segments, rather than sampling isolated windows, ensured that movement estimates reflected the full temporal organisation of fetal activity.

Operational definitions prioritised observable kinematic features, including movement amplitude, coordination, speed, and anatomical involvement, to maximise reliability and reduce subjective inference. When movements were partially obscured by fetal position, acoustic shadowing, or image degradation, events were coded only when sufficient visual evidence was available to support confident classification. Ambiguous or indeterminate activity was conservatively excluded to minimise overestimation of behavioural frequency. This approach reduced misclassification and maintained consistency across recordings with variable image quality.

To support subsequent analyses, raw frame annotations were aggregated into derived indices for each baseline and stimulus period, including total movement frequency, cumulative duration, and the proportion of time spent active. These indices provided standardised metrics of motor output that could be compared across conditions and gestational ages.

FBM measures were subsequently interpreted in conjunction with independently coded FEM and higher-order FBS classifications, allowing differentiation between general changes in motor activation and state-dependent or modality-specific behavioural modulation. Metadata likely to influence observability or responsiveness, including fetal position, fetal ear orientation, maternal tissue thickness, experimental order, and session time, were recorded for each file and cross-verified against ultrasound markers to facilitate contextual interpretation and quality control.

Table 2

Operational Definitions of Fetal Behaviours Coded Using the Behavioural Ethogram

Behaviour	Code	Operational Definition
General movements	GM	Complex, variable, and fluent movements involving the trunk and multiple limbs, characterised by gradual onset and offset and changing direction, reflecting spontaneous motility rather than reflexive action.
Isolated limb movements	IL	Discrete movements of a single limb without concurrent trunk or whole-body involvement.
Jaw movements	JM	Rhythmic or discrete opening and closing of the jaw without concurrent sucking or swallowing.
Yawn	Y	A slow, wide opening of the mouth followed by a gradual closure, often accompanied by head extension.
Sucking	K	Repetitive rhythmic mouth movements resembling postnatal sucking behaviour, sometimes associated with hand-to-mouth contact.
Swallowing	W	A distinct pharyngeal movement following jaw opening, often temporally linked to sucking.
Startle	SA	A sudden, brief, high-amplitude movement involving rapid extension or flexion of the trunk and/or limbs, with abrupt onset and offset, typically occurring as a single event and lacking sustained movement coordination.
Hiccup	HI	Short, repetitive jerking movements of the diaphragm or trunk occurring in rapid succession, typically rhythmic and stereotyped.
Stretch	ST	A slow, sustained extension of the trunk and/or limbs, often involving axial elongation and increased muscle tone.
Hand-to-mouth	M	Directed movement of the hand towards the mouth region, with or without contact.
Hand-to-face	F	Directed movement of the hand towards the face, excluding the mouth.
Head rotation	RO	Lateral turning of the head along the horizontal axis.
Head flexion	RF	Forward bending of the head towards the chest.
Head anteflexion	AF	Sustained forward head posture indicating prolonged neck flexion, often associated with alert or attentive behavioural states.

Coding of FEM

FEM were selected as the primary behavioural marker due to their established association with behavioural state organisation, sensory gating, and emerging attentional mechanisms, rendering them particularly informative for testing hypotheses concerning selective engagement. In Studies 1 and 2, FEM were coded from the transverse ultrasound plane using anatomical reference points, including the nasion, orbital sockets, and midline cranial structures, to ensure consistent lens tracking and spatial orientation (Appendix C).

Eye movements were classified using an operationally refined version of the Birnholtz (1981) typology. FEM were defined as observable displacements of the fetal lens from a stationary position to a subsequent stationary point within the orbital socket, with movement onset coded at the first detectable displacement and offset defined as cessation of motion in that direction (Birnholtz, 1981; Woitek et al., 2013). Movements were coded as lateral or medial relative to the facial midline and treated as discrete behavioural events. Segments in which more than 50% of frames were not codable were excluded to preserve measurement validity.

To enhance definitional clarity and reliability in contemporary high-resolution datasets, the historically ambiguous Type III category was excluded. Five operational categories were retained: Type I, rapid movement followed by slower return; Type II, single slow movement; Type IV, repetitive rapid bidirectional movements exhibiting a nystagmoid profile; and Type V, a residual category capturing patterns not conforming to the preceding definitions.

All FEM coding was conducted from transverse-plane recordings, which provide stable cross-sectional visualisation of the orbital sockets and medial–lateral trajectories and offer superior spatial resolution for detecting multidirectional and rapid oculomotor activity compared with alternative planes (Woitek et al., 2013).

Reliability and Validity

To support coding reliability across both studies, a structured coding manual was employed, and we completed formal training and calibration sessions prior to the commencement of formal coding. Calibration meetings were held to align interpretive criteria and to minimise systematic drift over time. Interrater reliability was assessed through independent double-coding of a predefined subset of recordings (10% of the dataset), sampled at both the beginning and end of the coding period, to evaluate consistency and detect drift.

Interrater agreement was quantified using Cohen's kappa (Cohen, 1960). Coding proceeded only after coders achieved $\kappa \geq .80$, indicating substantial agreement. Discrepant classifications were resolved through discussion and consensus, and ambiguous events were documented in an event log for subsequent review. This reliability framework was intended to strengthen behavioural validity by ensuring that coded events reflected observable fetal behaviour rather than rater inference. Reliability coefficients exceeded thresholds typically considered acceptable for behavioural research, supporting the robustness of the coding framework.

Data Processing and Quantitative Analyses

Behavioural data were exported from *The Observer XT 16 (version 16)* as time-stamped event logs and processed using R (version 4.3.0). Analyses were conducted separately for Study 1 and Study 2 but followed a shared analytic logic centred on within-subject comparison and baseline control. Behavioural data were structured hierarchically at the participant, condition (baseline versus stimulus), and behavioural category (FEM, FBM, and FBS). For each predefined segment, behavioural frequencies and durations were extracted, and time-series representations were generated where temporal patterning was analytically relevant. All inferential tests were two-tailed with $\alpha = .05$.

Baseline and stimulus epochs were segmented a priori using standardised temporal windows aligned to stimulus onset and offset markers. Where possible, segments were of equal duration to permit direct comparison across conditions. In instances where minor variation in segment length occurred due to ultrasound obstruction or fetal repositioning, behavioural frequencies were normalised to rate-based indices (events per minute) to control for differences in observation time. This procedure ensured that estimates of behavioural frequency and temporal organisation reflected genuine condition-related effects rather than artefacts arising from unequal sampling durations.

Prior to analysis, datasets were screened for completeness, coding accuracy, and distributional assumptions. Missing data arising from brief ultrasound obstruction or fetal repositioning were minimal and judged to be random; therefore, no imputation procedures were applied. Outliers were inspected descriptively and retained unless attributable to clear recording artefacts. Interrater reliability thresholds ($\kappa \geq .80$) were verified before analysis to ensure behavioural validity.

Phase 1: Behavioural Coding and Quantification

Frame-by-frame behavioural coding was conducted using a structured ethogram to quantify fetal behavioural states, fetal eye movements, and fetal body movements. Coding and data processing were undertaken over eight months and comprised approximately 400 hours of systematic analysis, including primary annotation (≈260 hours), independent double-coding and adjudication (≈80 hours), and data cleaning and quality assurance procedures (≈60 hours).

During baseline epochs, defined as non-experimental periods of the ultrasound recordings, observable fetal eye movements were identified and coded for all participants. Coding required careful discrimination of oculomotor activity, with particular attention to lens visibility and orientation. Only lateral and medial eye movements were eligible for

classification into specific FEM types. Head and hand movements were coded independently of lens visibility to ensure comprehensive behavioural capture. Frequencies of each behavioural category were then quantified for each participant and condition.

Behavioural annotation and data management were conducted using *The Observer XT*, which enabled high-resolution, frame-by-frame coding and efficient retrieval and export of variables. Because accurate identification of the fetal lens required continuous visual inspection, full blinding to condition was not feasible; however, this limitation was mitigated through structured calibration, senior researcher oversight, and systematic validation checks.

Phase 2: Temporal Organisation Analyses

To characterise behavioural organisation beyond aggregate frequency measures, DTW was used to quantify similarity between baseline and stimulus-linked behavioural time series. DTW accommodates variability in response latency, tempo, and duration, enabling comparison of sequences that are temporally misaligned but structurally similar. This approach reduces the risk of misclassifying delayed or temporally extended responses as absent when using strictly time-locked analyses.

Behavioural event streams were converted into binary or count-based time series at fixed temporal resolution, and within-subject comparisons were conducted between baseline and stimulus segments. Euclidean distance was used as the similarity metric, with a Sakoe–Chiba warping window constrained to 10% of sequence length to limit excessive temporal distortion. A symmetric step pattern was applied, and DTW distances were normalised by path length to permit comparison across sequences of differing duration. Larger DTW values indicated greater divergence between baseline and stimulus organisation. DTW indices were interpreted alongside conventional frequency-based measures. All processing steps and

analytical scripts were version-controlled and retained to provide an audit trail from raw exports to the final analytical datasets.

Analysis Data and Diagnostics

Study 1

Study 1 examined baseline organisation of FEM within behavioural state context and assessed developmental and stimulus-linked variation in movement complexity. Associations between FEM types and FBS were evaluated using chi-square tests of independence, with standardised residuals used to identify over- and under-represented pairings. Effect size was reported using Cramer's V.

Within-subject contrasts compared behavioural frequencies and DTW distances between baseline and stimulation periods, using paired-samples t tests when assumptions of normality were met and Wilcoxon signed-rank tests otherwise. Developmental variation was examined using gestational age as a continuous predictor in correlational and mixed-effects modelling frameworks.

To account for repeated observations within fetuses, generalised linear mixed-effects models were fitted with fetus identity specified as a random intercept. Behavioural state and condition were entered as fixed effects, and gestational age was included as a covariate. Model coefficients were reported with corresponding odds ratios and 95% confidence intervals.

Study 2

Study 2 evaluated discriminative behavioural responses to musical timbre and harmonic modality relative to baseline. Behavioural frequencies and durations were extracted for baseline, timbre, and harmony conditions. Linear and generalised linear mixed-effects models were fitted using the *lme4* package in R, with fetus identity specified as a random intercept to

account for within-subject dependency. Condition was entered as a fixed effect, and gestational age and maternal tissue thickness were explored as covariates where relevant.

Response categories were compared across conditions using chi-square analyses with Cramer's V reported as an index of effect size. Planned within-subject contrasts compared coordinated FEM–FBM responses, latency to onset, and response duration between auditory conditions using paired-samples t tests or non-parametric equivalents where required. Cohen's d and confidence intervals were reported.

Mixed-effects models were further fitted to predict coordinated engagement (FETA) and DTW distance from stimulus condition, with fetus identity included as a random intercept and gestational age as a covariate. Fixed effects were evaluated using likelihood-ratio tests and Wald statistics. Where multiple related contrasts were conducted, Holm–Bonferroni corrections were applied. Model diagnostics included inspection of residual distributions, Q–Q plots, convergence, and fitted values. Continuous predictors (e.g., gestational age) were mean-centred to improve interpretability and reduce multicollinearity, and random-intercept models were used as the primary specification given the limited number of repeated observations per fetus. Influential observations were assessed using fitted-versus-categorical diagnostics and, where applicable, by inspecting leverage or influence measures.

To minimise Type I error inflation, corrections were applied within pre-specified families of related contrasts, while primary hypotheses were evaluated using planned comparisons. Across both studies, effect sizes and 95% confidence intervals were reported, and analytic decisions regarding exclusions, thresholds, and parameters were specified a priori or justified with reference to contemporary methodological standards. Response latency was defined as the time from stimulus onset marker to the first coded behavioural event meeting

response criteria, and response duration was defined as the total time from response onset to offset within the stimulus window.

Ethical Considerations

Ethical approval was obtained from the New Zealand Health and Disability Ethics Committee for both studies (Study 1: Reference No. 2021 EXP 1152; Study 2: Reference No. 19197). Participation was voluntary, participants were informed of their right to withdraw without penalty, and all participants gave informed consent. Written informed consent was obtained prior to data collection, and participants were given opportunities to ask questions before and during participation. Maternal comfort and fetal well-being were monitored throughout the scan, and sessions were discontinued immediately upon the participant's request or clinical indication. All stimulus parameters were selected to remain within established prenatal safety guidelines for ultrasound exposure and external auditory stimulation (Abramowicz, 2007; Committee on Environmental Health, 1997; Graven, 2000).

All data were de-identified prior to coding and analysis. Identifying materials (e.g., consent forms and questionnaires) were stored separately from coded data in secure university facilities. Digital files were stored on password-protected and encrypted devices with restricted access. Data will be retained for ten years in accordance with institutional policy, after which files will be destroyed. Secondary analysis was conducted in accordance with institutional guidelines governing data confidentiality, participant anonymity, and responsible research conduct. No additional risk was posed to participants, and all procedures were disclosed.

For presentation within this thesis, the documents used in Study 1 and Study 2, including the Participant Information Sheet, consent form, debriefing information, and statements regarding data handling, were recreated for illustrative purposes. These recreated materials were designed to closely reflect the structure, content, and ethical requirements of the

original documents that received formal ethics approval for each study. No original participant documents or identifying information are reproduced. The recreated materials are included solely to provide transparency regarding study procedures, participant rights, and data management practices, and should not be interpreted as the original ethics-approved materials. The appropriate ethics committee granted ethical approval for both studies. Additionally, access to identifiable or coded data was limited to the research team listed on the ethics approval. (Appendix A).

Māori and Cultural Considerations

Consistent with the University of Waikato's commitment to Te Tiriti o Waitangi, recruitment and consent processes were designed to be culturally safe, inclusive, and responsive to whānau involvement. Participants in both studies were welcomed to include whānau support during study discussions, provided with materials to share with family members, and offered a koha in recognition of their contribution. To support accessible and informed consent, key study information was provided both verbally and in writing, with additional discussion available upon request to accommodate diverse communication preferences.

Knowledge generated through participation was treated as taonga, and participants were provided with a summary of the findings upon completion of the analysis to support reciprocity and transparency. Consistent with principles of tikanga-informed practice and Māori data sovereignty, participant information was treated as collectively significant rather than solely individual property. All data were handled respectfully, stored securely, accessed only by authorised researchers, and used exclusively for the purposes outlined in consent documentation, with data management practices prioritising confidentiality, participant autonomy, and collective wellbeing.

Results

Results are reported separately for Study 1 and Study 2, followed by an integrative analysis of temporal behavioural organisation. All analyses used two-tailed significance testing with $\alpha = .05$.

Preliminary Analyses

Data Screening and Assumptions

Data from Study 1 and Study 2 were screened for completeness, coding accuracy, outliers, and distributional assumptions prior to inferential analysis. Prior to hypothesis testing, the data were screened to assess the assumptions underlying the planned statistical analyses. Missing data were minimal and arose primarily from brief ultrasound obstructions or transient fetal repositioning; examination of missingness patterns, including Little's Missing Completely at Random (MCAR) test, indicated that data were missing at random (χ^2, ns), justifying the use of listwise deletion without introducing systematic bias (Little, 1988).

Visual inspection of histograms and Q–Q plots revealed no substantive departures from normality across key behavioural measures, with only mild positive skew observed in some frequency variables, consistent with low baseline fetal movement rates; skewness and kurtosis values remained within acceptable limits for parametric analysis (Appendix B). Homogeneity of variance was assessed using Levene's tests and corresponding visual diagnostics, with no evidence of meaningful heteroscedasticity across gestational age groups or experimental conditions (Appendix B).

To further evaluate analytic robustness, parallel non-parametric analyses were conducted and yielded convergent results. Collectively, these screening procedures indicate

that the data met the assumptions required for inferential analyses and that observed effects are unlikely to reflect artefacts arising from distributional irregularities or data quality limitations.

Interrater Reliability

Interrater reliability was assessed for behavioural coding using a randomly selected subset comprising 25% of Study 1 recordings. Two trained coders independently coded fetal eye movements, body movements, head orientation, startles, and periods of stillness. Agreement was high across all behavioural variables, with Cohen's $\kappa = .93$ (95% CI [.79, .87]), $p < .001$, indicating excellent reliability and supporting the internal validity of the behavioural coding framework.

Study 1: Fetal Eye Movements and Behavioural State

Distribution of Fetal Eye Movement Types Across Behavioural States

Descriptive analyses examined the distribution of fetal eye movement (FEM) types across all baseline observations. Type II movements accounted for the largest proportion of coded events (39.69%), followed by Type V (36.55%) and Type IV (15.99%). Type I movements were least frequent (7.76%). Cross-tabulation of FEM types by FBS revealed distinct state-dependent distributions (see Table 3).

As shown in Figure 1, higher-order FEM types (II and IV) were more prevalent during Active Sleep (2F), Transitional (3F), and Quiet Awake (4F), whereas Type I FEM predominated during Quiet Sleep (1F). Chi-square analyses and standardised residuals confirmed that these distributions differed significantly across behavioural states, supporting state-dependent organisation of oculomotor activity.

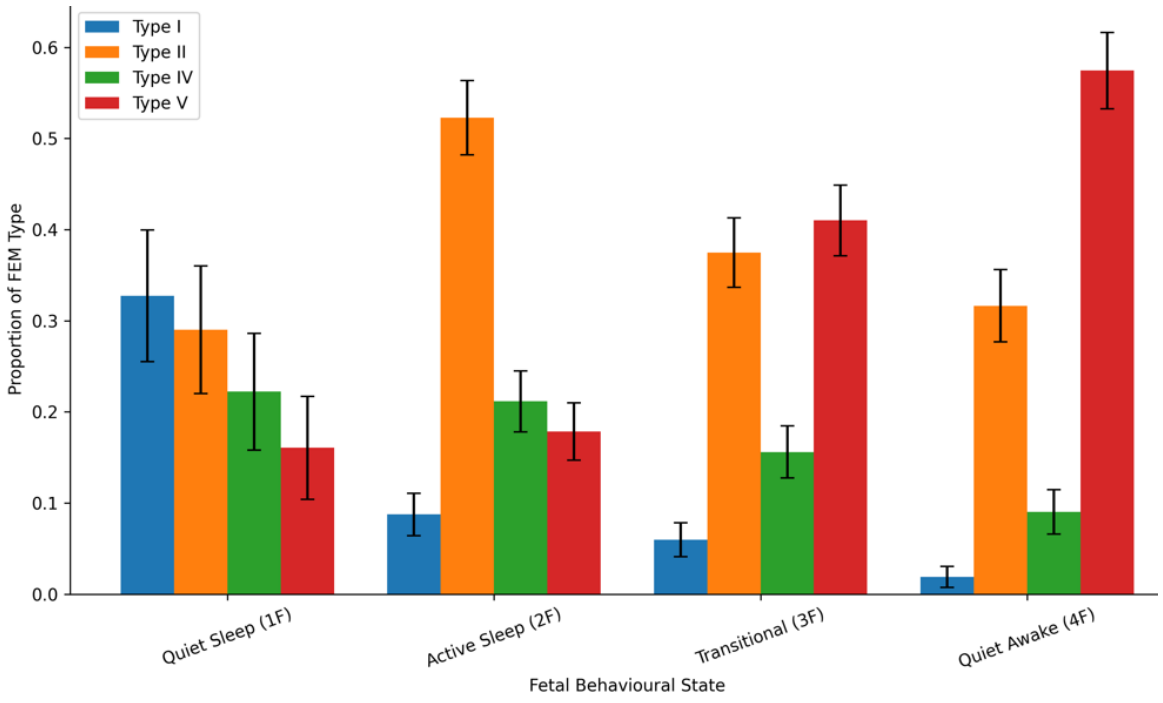
Table 3

Distribution of Fetal Eye Movement (FEM) Types Across Fetal Behavioral States (FBS)

Fetal Behavioural State	Type I	Type II	Type IV	Type V
Quiet sleep (1F)	53	47	36	26
Active sleep (2F)	50	299	121	102
Transitional (3F)	37	233	97	255
Quiet Awake (4F)	10	168	48	305
Total	146	747	301	688

Figure 1

Distribution of Refined Fetal Eye Movement (FEM) Types Across Fetal Behavioural States (FBS) During Baseline Recording



Note. Type III FEM was excluded due to insufficient definitional clarity and its absence in contemporaneous ultrasound data.

A chi-square test of independence revealed a significant association between FEM type and behavioural state, $\chi^2(9, N = 1{,}882) = 431.62$, $p < .001$, with a medium-to-large effect size (Cramer's V = .34), indicating a meaningful relationship between behavioural state and oculomotor patterning. Here, N denotes the total number of codable FEM events observed across baseline epochs, rather than the number of participants, so that the analysis captures event-level distributions of eye movement types within behavioural states.

Assumptions for the chi-square analysis were satisfied. All expected cell frequencies exceeded minimum recommended thresholds, no cells contained expected counts below five, and no pooling or continuity corrections were required. The contingency table, therefore, met the distributional requirements for valid chi-square testing.

Examination of adjusted standardised residuals indicated that the overall association was characterised by systematic deviations from independence across multiple state–movement pairings. Complex FEM types (Types II and V) occurred more frequently than expected in Active Sleep (2F), Transitional (3F), and Quiet Awake (4F), and less frequently than expected in Quiet Sleep (1F). Conversely, lower-complexity FEM types were observed more frequently than expected in Quiet Sleep and less frequently than expected in higher-arousal states. These deviations were distributed across several cells of the contingency matrix rather than being confined to a single pairing (see Table 4).

Overall, the distribution of FEM types varied significantly across behavioural states at baseline, with event-level frequencies differing from expected counts under the assumption of independence.

Collectively, this pattern is consistent with state-dependent modulation of oculomotor behaviour and supports the interpretation that complex eye movements are preferentially expressed during periods of heightened behavioural activation. Methodologically, these findings reinforce the importance of modelling behavioural state when interpreting FEM activity, as aggregation across states would obscure meaningful organisation in oculomotor complexity and risk misattributing endogenous state effects to stimulus responsiveness.

Table 4

Standardised Categories for FEM Types Across Fetal Behavioural States

FBS	Type I	Type II	Type IV	Type V
Quiet sleep (1F)	5.17**	−4.03**	−4.61**	−5.88**
Active sleep (2F)	−0.16	8.03**	3.08*	−2.63†
Transitional (3F)	−1.61	0.47	−0.76	4.89**
Quiet Awake (4F)	−3.81**	−0.18	2.59†	7.41**

Note. Positive values indicate observed cell frequencies greater than expected under independence; negative residuals indicate observed frequencies lower than expected. Larger absolute values indicate a stronger contribution of the cell to the overall χ^2 statistic. † $p < .10$. * $p < .05$. ** $p < .01$. *** $p < .001$.

Developmental Variation of Complex FEM Responsiveness During Stimulation

To quantify developmental variation in stimulus-linked oculomotor behaviour, the association between gestational age (in days) and the proportion of complex fetal eye movements (FEM Types II–IV) observed during experimental conditions was examined using a Pearson product–moment correlation. The proportion of complex FEM was operationalised at the participant level as the number of Type II–IV movements divided by the total number of codable FEM recorded during stimulation, thereby standardising estimates relative to individual differences in overall movement frequency. This proportional metric reduced potential confounding arising from variation in total behavioural output and enabled comparison of oculomotor complexity across fetuses.

Preliminary inspection of scatterplots and residual diagnostics supported the assumptions of linearity, homoscedasticity, and absence of influential outliers, justifying the

use of a parametric correlational approach. The analysis revealed a statistically significant positive association between gestational age and the proportion of complex FEM (r = .32, 95% CI [.02, .57], p = .041). Within the sampled late third-trimester window (33–37 weeks), fetuses of greater gestational age exhibited relatively higher proportions of complex oculomotor patterns during stimulation. This magnitude corresponds to a small-to-moderate effect, consistent with gradual maturational change rather than abrupt developmental transition.

To contextualise these developmental trends within behavioural organisation, Table 5 integrates FEM distributions, standardised categories, and proportions of complex FEM across behavioural states. Complex FEM profiles were more frequently observed during higher-arousal states, particularly Active Sleep and Quiet Awake, relative to Quiet Sleep. This state-dependent distribution underscores the importance of interpreting developmental changes in oculomotor complexity within a behavioural-state context. It supports the analytic strategy of modelling state as a covariate when evaluating stimulus-linked engagement (see Appendix C).

Table 5

Distribution of FEM Across Behavioural States and Developmental Responsiveness

FBS Type	Type I (n)	Type II (n)	Type IV (n)	Type V (n)	Row Total	Standardised Types (I, II, IV, V)	% Type II–IV (Stimulus-Linked)
Quiet Sleep (1F)	53	47	36	26	162	5.17**, −4.03**, −4.61**, −5.88**	22.22%
Active Sleep (2F)	50	299	121	102	572	−0.16, 8.03**, 3.08*, −2.63†	21.15%
Transitional (3F)	37	233	97	255	622	−1.61, 0.47, −0.76, 4.89**	15.59%
Quiet Awake (4F)	10	168	48	305	531	−3.81**, −0.18, 2.59†, 7.41**	9.05%
Total	146	747	302	688	1,887	—	17.41%

Note. % Type II–IV represents the proportion of complex FEMs observed within each behavioural state. Standardised residuals indicate deviations from expected frequencies. † $p < .10$. * $p < .05$. ** $p < .01$. *** $p < .001$.

To further examine whether FEM complexity was systematically organised as a function of FBS, a binomial generalised linear mixed-effects model was fitted to predict the likelihood of complex FEM (Types II–IV). The dependent variable was coded at the event level as a binary outcome (complex vs non-complex), enabling estimation of the probability that a given movement exhibited higher-order oculomotor complexity. A logit link function was specified, consistent with the binomial error structure. FBS was entered as a categorical fixed effect, with Quiet Sleep (1F) specified a priori as the reference category to permit interpretation relative to the lowest-arousal state. Gestational age (in days) was included as a continuous covariate to account for developmental change across the late third trimester.

A random intercept for fetus identity was specified to account for repeated observations within individuals and to control for within-fetus dependency, thereby improving parameter estimation and avoiding inflation of Type I error associated with non-independent observations. The model revealed a significant overall effect of behavioural state on the likelihood of complex FEM, $\chi^2(3) = 94.21$, $p < .001$, indicating that oculomotor complexity varied systematically across states rather than being uniformly distributed. Relative to Quiet Sleep, the odds of complex FEM were significantly higher during Active Sleep, Transitional, and Quiet Awake states (see Table 6), consistent with greater behavioural activation and sensory engagement in these states.

Gestational age showed a small but statistically significant positive association with complex FEM likelihood, suggesting a gradual developmental increase in oculomotor complexity across the sampled gestational window. Diagnostic checks indicated satisfactory model fit, with no evidence of convergence issues or influential outliers.

Table 6

Generalised Linear Mixed Model Predicting Complex Fetal Eye Movements (Types II–IV)

Predictor	*b*	*SE*	*z*	*p*	OR	95% CI for OR
Intercept (Quiet Sleep)	−1.42	0.21	−6.76	< .001	0.24	[0.16, 0.36]
Active Sleep (2F)	1.18	0.19	6.21	< .001	3.26	[2.25, 4.72]
Transitional (3F)	0.64	0.17	3.76	< .001	1.90	[1.35, 2.66]
Quiet Awake (4F)	1.36	0.22	6.18	< .001	3.90	[2.54, 6.01]
Gestational age (days)	0.03	0.01	2.14	.032	1.03	[1.00, 1.06]

Note. A binomial generalised linear mixed-effects model was fitted with complex fetal eye movements (Types II–IV) as the outcome. Quiet Sleep (1F) served as the reference category for fetal behavioural state. A random intercept for fetus identity was included. OR = odds ratio; CI = confidence interval.

Study 2: Discriminative Auditory Engagement

Study 2 examined whether fetuses exhibited differential behavioural responses to complex auditory features, specifically musical timbre (string versus piano) and harmonic modality (minor versus major chords). Analyses focused on stimulus-linked behavioural responses relative to baseline.

Behavioural Response Profiles Across Auditory Conditions

Behavioural responses were classified into four mutually exclusive categories: FEM only, FEM accompanied by body movement, body movement only, and no observable response. A chi-square test of independence revealed a significant association between auditory condition and behavioural response category, $\chi^2(12, N = 250) = 34.67$, $p < .001$, with a small-to-moderate effect size (Cramer's V = .21). Response distributions differed systematically across baseline and auditory stimulation conditions (see Table 7). Baseline segments were characterised primarily by the absence of observable responses, whereas auditory stimulation conditions elicited higher proportions of coordinated FEM and body movement responses.

Table 7

Frequency of Fetal Behavioural Responses by Condition (N = 50)

Condition	FEM only	FEM + Body	Body only	No response
Baseline	12	8	5	25
String (Timbre)	8	22	6	14
Piano (Timbre)	10	15	7	18
Major (Chord)	11	16	6	17
Minor (Chord)	7	21	5	17

Note. FEM + Body = coordinated FETA responses.

Paired Comparisons of Discriminative Responses

To evaluate within-subject discriminative behavioural responses across auditory conditions, paired-samples *t-tests were conducted to compare coordinated FEM–FBM response frequencies between timbre (string vs. piano) and harmonic modality (minor vs.* major) conditions. Coordinated responses were operationalised as instances in which a fetal eye movement and body movement occurred within the predefined response window following stimulus onset. Preliminary inspection of difference-score distributions and Q–Q plots supported the assumptions of normality for paired comparisons. Response frequencies were expressed as proportional indices relative to total stimulus exposures to ensure comparability across participants.

A significant difference emerged between timbre conditions, with higher coordinated response frequencies observed during the string condition ($M = 0.79$, $SD = 0.18$) relative to the piano condition ($M = 0.62$, $SD = 0.18$), $t(22) = 2.71$, $p = .012$, Cohen's $d = 0.55$, 95% CI [0.04, 0.30]. This effect represents a moderate within-subjects difference, indicating greater behavioural engagement with string timbre than with piano timbre.

Similarly, harmonic modality contrasts revealed significantly higher coordinated response frequencies during minor chord presentations ($M = 0.83$, $SD = 0.17$) compared with major chord presentations ($M = 0.68$, $SD = 0.17$), $t(22) = 2.19$, $p = .038$, Cohen's $d = 0.45$, 95% CI [0.01, 0.29]. This effect was small to moderate in magnitude and suggests selective modulation of behavioural responsiveness by harmonic structure.

Temporal Characteristics of Behavioural Responses

To further characterise the dynamics of coordinated responding, paired-samples *t* tests examined differences in latency to response onset and total response duration across auditory

conditions. Latency was defined as the interval between stimulus onset and the first coordinated behavioural event, and duration was defined as the total time from onset to offset of the coordinated response within the stimulus window.

Latency to response onset did not differ significantly between the string timbre (M = 1.12 s, SD = 0.25) and piano timbre (M = 1.36 s, SD = 0.30) conditions, $t(22) = 2.02$, $p = .055$, Cohen's $d = 0.41$, indicating a trend toward faster responding to string stimuli that did not reach conventional significance thresholds.

In contrast, response duration differed significantly between harmonic modality conditions, with longer coordinated responses observed during minor chord presentations (M = 2.48 s, SD = 0.63) relative to major chord presentations (M = 1.97 s, SD = 0.58), $t(22) = 2.32$, $p = .029$, Cohen's $d = 0.48$. This moderate effect suggests sustained behavioural engagement in response to minor harmonic structures.

Temporal Reorganisation of Behaviour: Dynamic Time Warping and FETA

DTW was employed to quantify temporal divergence between baseline behavioural sequences and stimulus-evoked behavioural organisation. Unlike aggregate frequency measures, which index only how often behaviours occur, DTW captures the structure and timing of behavioural sequences by aligning event streams non-linearly and estimating the cumulative distance between patterns. Consequently, larger DTW distances reflect greater reorganisation of behavioural timing relative to baseline state structure rather than merely increased movement frequency or intensity.

Mean DTW distances varied systematically across auditory conditions, with the greatest divergence observed during string timbre and minor chord presentations and comparatively smaller divergence during piano timbre and major chord conditions (see Table

8). These differences indicate that certain acoustic features elicited greater restructuring of behavioural organisation than spontaneous baseline activity. Visual inspection of condition-level means further suggested a monotonic relationship between DTW distance and FEM–body coordination (FETA%), such that conditions with greater temporal divergence were associated with higher proportions of coordinated multimodal responses.

Figure 2 illustrates the convergence between DTW-derived temporal reorganisation and coordinated behavioural engagement across conditions. This correspondence indicates that increases in behavioural responsiveness were not limited to simple increases in event frequency but were accompanied by systematic changes in the temporal coupling and sequencing of eye and body movements. Collectively, these findings support the interpretation that specific acoustic features elicited selectively integrated and temporally organised behavioural responses, consistent with state-dependent sensory engagement rather than generalised arousal or non-specific motor activation.

Table 8

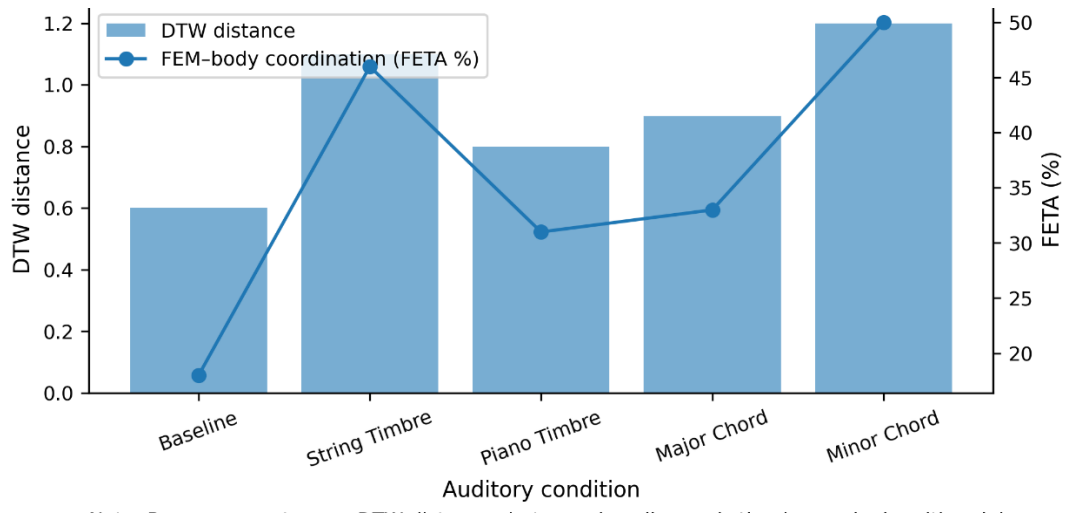
DTW Dissimilarity Between Baseline and Stimulus-Evoked Multimodal Profiles by Condition

Auditory Condition	DTW Distance (SD)	FEM–Body Coordination (FETA%)	Dominant Behaviours Contributing to Dissimilarity	Interpretation of Engagement
Baseline (No stimulus)	0.42 (0.11)	18.6%	GM, IL, HI	Predominantly spontaneous activity; low multimodal integration
String Timbre	0.87 (0.19)	46.3%	FEM II–IV + GM, M, F, RO	High divergence; coordinated oculomotor–somatic response
Piano Timbre	0.63 (0.16)	31.2%	FEM II + IL, JM	Moderate reconfiguration; weaker multimodal coupling
Minor Chord	0.91 (0.21)	49.8%	FEM IV + GM, ST, M, AF	Strongest divergence; sustained integrated profile
Major Chord	0.66 (0.18)	33.5%	FEM II + GM, IL	Moderate engagement; less persistent coordination

Note. Mean DTW distances and corresponding proportions of temporally aligned fetal eye movement–body movement epochs (FETA%) are summarised for each auditory condition. Higher DTW values indicate greater temporal reorganisation of behavioural activity relative to baseline, rather than simply higher movement frequency. Across conditions, larger DTW distances were consistently associated with higher FEM–body coordination, indicating convergence between temporal and multimodal indices of engagement. Minor-chord and string timbre conditions produced the greatest divergence from baseline and the highest coordination levels, whereas piano timbre and major-chord conditions showed more moderate reorganisation. This pattern suggests that specific acoustic features elicit selectively integrated behavioural responses rather than generalised motor activation.

Figure 2

Dynamic Time Warping (DTW) Distance and FEM-Body Coordination (FETA) Across Auditory Conditions



Note. Bars represent mean DTW distances between baseline and stimulus-evoked multimodal behavioural sequences, with higher values indicating greater temporal reorganisation relative to baseline. The overlaid line represents the proportion of stimulus epochs with temporally coordinated fetal eye and body movements (FETA), indicating multimodal sensory engagement. String timbre and minor-chord conditions exhibit the greatest divergence from baseline and the highest levels of coordinated engagement.

Fetal Evoked Transitory Arousal (FETA), operationalised as temporally coordinated occurrences of fetal eye and body movements within the predefined post-stimulus response window, served as an index of multimodal behavioural engagement. FETA proportions were calculated at the participant level as the percentage of stimulus epochs in which coordinated oculomotor–somatic activity was observed, thereby standardising engagement estimates across individuals and conditions.

Descriptively, FETA occurred most frequently during string timbre (46.3%) and minor chord (49.8%) conditions, compared with piano timbre (31.2%) and major chord (33.5%). Conditions associated with higher FETA proportions were also characterised by a greater co-occurrence of complex FEM patterns and coordinated body movements.

This pattern mirrors the DTW findings, whereby conditions that elicited stronger multimodal coordination also showed greater temporal divergence from baseline structure. Together, these convergent indicators suggest that specific acoustic features elicited selective and coordinated behavioural engagement rather than generalised motor activation. Additional illustrative examples of baseline–stimulus alignment across conditions are provided (Appendix C).

To formally evaluate whether behavioural engagement varied with auditory stimulus properties while accounting for repeated observations within fetuses, a binomial generalised linear mixed-effects model was fitted to predict the likelihood of coordinated FEM–body engagement (FETA). Engagement was coded as a binary outcome (present vs. absent) at the epoch level, with a logit link function. Stimulus condition (timbre and harmonic modality) was entered as a categorical fixed effect, with baseline specified as the reference category. Gestational age was included as a continuous covariate to account for developmental variation, and a random intercept for fetus identity was specified to control for within-subject

dependency. The model revealed significant effects of the auditory condition on the likelihood of engagement (see Table 9).

Compared with baseline, exposure to string timbre and minor harmonic modality was associated with higher odds of coordinated engagement, whereas piano timbre and major modality produced smaller but still significant increases. Gestational age was again positively associated with engagement likelihood, although the effect size was modest, consistent with gradual developmental change across the late third trimester.

Table 9

Binomial Mixed-Effects Model Predicting Coordinated Engagement (FETA)

Predictor	***b***	***SE***	***z***	***p***	**OR**	**95% CI for OR**
Intercept (Baseline)	−1.56	0.24	−6.50	< .001	0.21	[0.13, 0.34]
String timbre	1.32	0.26	5.08	< .001	3.75	[2.27, 6.19]
Piano timbre	0.54	0.23	2.35	.019	1.72	[1.09, 2.71]
Minor chord	1.48	0.28	5.29	< .001	4.39	[2.53, 7.63]
Major chord	0.62	0.25	2.48	.013	1.86	[1.14, 3.04]
Gestational age (days)	0.02	0.01	1.97	.049	1.02	[1.00, 1.04]

Note. A binomial mixed-effects model was fitted to predict coordinated fetal eye movement–body engagement (FETA). Baseline served as the reference category for the stimulus condition. A random intercept for fetus identity was included. OR = odds ratio; CI = confidence interval.

To examine whether auditory stimulation altered the temporal organisation of fetal behaviour, a linear mixed-effects model was fitted to predict the DTW distance between the baseline and stimulus periods. DTW distance served as a continuous index of temporal

reorganisation, with larger values reflecting greater divergence in the sequencing and coordination of behavioural events relative to spontaneous baseline structure. Stimulus condition was entered as a categorical fixed effect with baseline specified as the reference category, and a random intercept for fetus identity was included to account for repeated observations within fetuses and the non-independence of within-subject measurements.

Auditory condition significantly predicted DTW distance (see Table 10), indicating systematic differences in behavioural organisation across stimulus types rather than uniform shifts in overall activity. Compared with baseline, string timbre and minor harmonic modality were associated with the largest increases in DTW distance, indicating the greatest temporal restructuring of multimodal behaviour. Piano timbre and major chord conditions produced smaller but still significant increases, consistent with more moderate reorganisation. Gestational age demonstrated a small but statistically significant positive association with DTW distance.

Diagnostic inspection of residuals and model fit indicated no violations of linearity or homoscedasticity assumptions. Collectively, these findings indicate that specific acoustic features elicit a selective temporal reorganisation of fetal behaviour rather than simply increasing movement frequency, supporting the interpretation of stimulus-dependent engagement.

Table 10

Linear Mixed-Effects Model Predicting Dynamic Time Warping (DTW) Distance

Predictor	***b***	***SE***	***t***	***p***	**95% CI**
Intercept (Baseline)	0.41	0.04	10.25	< .001	[0.33, 0.49]
String timbre	0.46	0.06	7.67	< .001	[0.34, 0.58]
Piano timbre	0.22	0.05	4.40	< .001	[0.12, 0.32]
Minor chord	0.50	0.07	7.14	< .001	[0.36, 0.64]
Major chord	0.24	0.06	4.00	< .001	[0.12, 0.36]
Gestational age (days)	0.004	0.002	2.00	.046	[0.00, 0.01]

Note. A linear mixed-effects model was fitted to predict the Dynamic Time Warping (DTW) distance between baseline and stimulus-evoked behavioural profiles. Baseline served as the reference category. A random intercept for fetus identity was included. Larger DTW values indicate greater temporal divergence from baseline.

To evaluate whether temporal reorganisation of behaviour was associated with coordinated multimodal engagement, a binomial generalised linear mixed-effects model was fitted predicting the likelihood of fetal evoked transitory arousal (FETA) from DTW distance. FETA was coded at the epoch level as a binary outcome (coordinated eye–body response present vs. absent), and a logit link function was specified to model the probability of engagement.

DTW distance was entered as a continuous predictor indexing the magnitude of temporal divergence between baseline and stimulus-evoked behavioural organisation. Gestational age was included as a continuous covariate to account for developmental variation, and a random intercept for fetus identity was specified to control for repeated observations within individuals and the resulting non-independence of responses.

DTW distance significantly predicted the likelihood of coordinated engagement (Table 11). Greater divergence between baseline and stimulus-evoked behavioural profiles was associated with markedly increased odds of FEM–body coordination. Specifically, each one-unit increase in DTW distance was associated with an approximately 6.6-fold increase in the odds of coordinated engagement (OR = 6.62, 95% CI [3.01, 14.56], $p < .001$).

Models were fitted in R using the *lme4* package with maximum likelihood estimation. Continuous predictors were retained at their original scales to preserve the interpretability of coefficients. Statistical significance for fixed effects was assessed using Wald z-tests, and odds ratios with corresponding 95% confidence intervals were derived by exponentiating the model coefficients.

Model diagnostics included inspection of convergence, residual patterns, and influence statistics to verify stability of parameter estimates and appropriateness of the specified random-effects structure. Gestational age again demonstrated a small but statistically significant positive effect, consistent with gradual developmental increases in engagement likelihood across the late third trimester. Diagnostic checks indicated satisfactory model convergence and no evidence of influential outliers.

Table 11

Binomial Mixed-Effects Model Predicting Coordinated Engagement (FETA) From DTW Distance

Predictor	*b*	*SE*	*z*	*p*	OR	95% CI for OR
DTW distance	1.89	0.41	4.61	< .001	6.62	[3.01, 14.56]
Gestational age (days)	0.02	0.01	2.01	.044	1.02	[1.00, 1.04]

Note. A binomial mixed-effects model was fitted to predict coordinated fetal engagement (FETA) from the Dynamic Time Warping (DTW) distance. A random intercept for fetus identity was included. OR = odds ratio; CI = confidence interval.

Discussion

Overview of Findings

This thesis examined whether fetal behavioural patterns during late gestation reflect organised sensory engagement with environmental stimulation, and whether engagement varies as a function of FBS, gestational age, and auditory stimulus characteristics. Across two interconnected studies, the results converge on three core conclusions. First, fetal behavioural evidence indicates that fetal responsiveness is state-modulated and baseline-contingent. Study 1 demonstrated a systematic, patterned organisation of FEM across behavioural states under baseline conditions, supporting FEM as a state-sensitive marker of fetal behavioural organisation rather than as random movement output (Hunter et al., 1982; Nijhuis et al., 1982).

Second, this behavioural organisation further differentiated across complex acoustic contrasts when internal state and spontaneous activity are explicitly controlled. Building on this foundation, Study 2 identified within-subject differences in coordinated FEM-plus-body responses and temporal response properties across contrasts in musical timbre and harmonic modality, consistent with evidence that fetal responses to stimulation depend on both stimulus properties and the functional context in which stimulation occurs (Lecanuet & Schaal, 1996).

Third, developmental change across the sampled window was modest but consistent, with increasing probability of complex and coordinated responding at later gestational ages, aligning with evidence that behavioural state organisation consolidates and becomes more stable toward late gestation (Nijhuis et al., 1982; Schneider & Prechtl, 1998).

Together, these findings address a central limitation of earlier prenatal work in which responsiveness is often assessed without baseline normalisation or explicit state control and extend fetal auditory research beyond detection paradigms by examining behaviour under acoustically structured, theoretically motivated contrasts.

Fetal Eye Movements and Behavioural State Interpretation

Study 1 tested whether FEM types were non-randomly distributed across fetal behavioural states under baseline conditions (H1). The Study 1 results provided strong evidence that FEM profiles are systematically organised by behavioural state. FEM type and FBS were significantly associated, $\chi^2(9, N = 1{,}882) = 431.62$, $p < .001$, with a medium-to-large effect (Cramer's V = .34). Standardised category patterns indicated that Quiet Sleep (1F) was characterised by a higher-than-expected frequency of Type I and lower-than-expected frequencies of higher-order movements (Types II, IV, V). In contrast, Active Sleep (2F) and Quiet Awake (4F) showed the opposite pattern, with elevated complex FEM frequencies.

The observed association between FEM profiles and FBS indicates that oculomotor activity varies systematically with behavioural state organisation rather than reflecting stochastic movement output. This pattern is consistent with state-based models of fetal behaviour, in which states reflect coordinated central nervous system organisation and the gating of motor expression and responsiveness (Lecanuet et al., 2000; Nijhuis et al., 1982). This finding also provides a methodological foundation for interpreting stimulus-linked change: if FEM patterns differ across states under baseline conditions, then state distribution must be treated as a plausible alternative explanation for apparent stimulus effects unless explicitly controlled (Lecanuet & Schaal, 1996; Nijhuis et al., 1982).

A further strength of Study 1 is the refined FEM typology approach employed in this thesis, which is compatible with contemporary imaging constraints and interpretive clarity by avoiding historically ambiguous categories that have demonstrated limited reproducibility in modern ultrasound contexts. In this context, excluding poorly defined classifications reduces the risk of misclassification. It improves comparability across datasets, consistent with recommendations that fetal behavioural inference should prioritise reliability and construct clarity when measurement constraints apply (Reid & Dunn, 2021).

Classical ultrasound research has established that FEMs increase in complexity throughout gestation and are detectable from mid-gestation onward, with slow eye movements evident early and rapid eye movements emerging later, with frequency increasing during the second half of gestation (Birnholtz, 1981). Overall, Study 1 supports the proposition that FEM patterns can be treated as meaningful behavioural correlates of state organisation in late gestation, thereby addressing concerns in earlier observational work in which absent or reduced responsiveness was interpreted without a state context.

Discriminative Auditory Engagement

Study 2 examined whether fetuses demonstrate discriminative behavioural responding to complex auditory features (H2). Study 2 extended fetal auditory research beyond detection-only paradigms by testing behavioural differentiation across musically structured contrasts and by prioritising coordinated multimodal responding. Behavioural response category differed significantly by condition, $\chi^2(12, N = 250) = 34.67$, $p < .001$ (Cramer's V = .21). Baseline periods were characterised by no observable response. In contrast, auditory conditions increased coordinated FEM + body movement responding, supporting the conclusion that stimulation altered the behavioural profile relative to spontaneous activity. Such baseline-dependent response patterns are consistent with evidence that fetal behavioural

and physiological reactions vary with both the properties of stimulation and the functional status of the fetus (Lecanuet & Schaal, 1996; Lecanuet et al., 2000).

Within-subject comparisons indicated significant discriminative patterning in the frequency of coordinated FEM-plus-body movement responses across timbre contrasts (string vs. piano) and harmonic modality contrasts (minor vs. major). Coordinated response frequency was higher for string vs piano timbre ($t(22) = 2.71$, $p = .012$, $d = 0.55$) and for minor vs major modality ($t(22) = 2.19$, $p = .038$, $d = 0.45$). Temporal analyses further indicated condition differences in duration (minor vs. major), whereas timbre latency differences did not reach conventional significance. Latency differences for timbre approached but did not meet conventional thresholds ($p = .055$), while response duration was longer for minor than major chords ($t(22) = 2.32$, $p = .029$, $d = 0.48$).

Together, these findings are consistent with the premise that both stimulus properties and internal constraints shape fetal auditory responsiveness, and that behavioural indicators can show structured differences when the analysis is baseline-referenced and within-subject (Lecanuet & Schaal, 1996; Reid & Dunn, 2021). These results extend prenatal auditory research that has focused on habituation, maternal voice recognition, or simple spectral contrasts by testing discrimination-relevant acoustic dimensions under controlled stimulation with baseline-referenced behavioural indices (DeCasper & Spence, 1986; Kisilevsky et al., 2004; Lecanuet & Granier-Deferre, 2017).

The measurement response system used in this thesis, particularly coordinated FEM-plus-body patterns, provides a more stringent behavioural index than isolated movement counts, as it captures multimodal coordination rather than undifferentiated activity. Fetal behavioural responses to sensory stimulation were characterised by substantial inter-individual variability, consistent with previous work on fetal attention and habituation

patterns (Hepper & Shahidullah, 1992; Van Heteren et al., 2001a). Rather than exhibiting uniform or linear increases in responsiveness, fetuses demonstrated a range of response profiles, including transient engagement, gradual decline in responding, and complete non-responsiveness. Importantly, such variability has been repeatedly observed among healthy fetuses and is not necessarily indicative of atypical development (Van Heteren et al., 2001).

A large proportion of fetuses showed minimal or no observable behavioural responses during experimental periods, a pattern previously attributed to behavioural state rather than reduced perceptual capacity (Hepper & Shahidullah, 1992; Piontelli, 2015). Periods of quiet sleep are associated with reduced motor output and attenuated responsiveness to external stimuli, despite continued neural-level sensory processing (Nijhuis et al., 1982; Lecanuet et al., 2000). Within this framework, the absence of overt FEM during certain epochs should not be interpreted as disengagement or sensory insensitivity, but rather as state-dependent suppression of behavioural expression.

Additionally, Study 2 results inferred that the pattern of declining behavioural responses observed across repeated stimulation is consistent with habituation-like processes previously documented in fetal research (Leader et al., 1982; Kuhlman et al., 1988; Morokuma et al., 2004). Evidence of response recovery following short breaks between stimulation periods further aligns with dishabituation effects reported in fetuses and newborns, indicating sensitivity to environmental change (Sandman et al., 1997). Although the present study was not designed to assess habituation formally, these response patterns are consistent with selective sensory engagement and early learning-like mechanisms operating in utero (Lecanuet & Granier-Deferre, 2017; Lecanuet & Schaal, 1996).

At the same time, the thesis makes an appropriately conservative claim: behavioural discrimination is not equivalent to specifying cortical representational mechanisms.

Behavioural differentiation can arise from feature processing, arousal modulation, or their interaction (Lecanuet & Schaal, 1996). However, two aspects of this pattern strengthen the discrimination interpretation relative to a pure "general arousal" account: (a) condition differences were observed within-subject across controlled contrasts, and (b) the strongest effects clustered in theoretically meaningful conditions (string timbre; minor modality) rather than scaling uniformly across all stimuli. Nevertheless, the presence of consistent within-subject differences under controlled presentation supports the conclusion that late-gestation fetal behaviour can exhibit stimulus-linked differentiation when assessed using state-informed, baseline-controlled methodology (Lecanuet et al., 2000; Reid & Dunn, 2021).

Developmental Effects Across Late Gestation

Developmental variation was assessed by examining whether stimulus-linked behavioural complexity covaried with gestational age within the sampled late-gestation window (H3). Study 1 showed a statistically significant but modest developmental trend. Gestational age correlated positively with the proportion of complex FEMs under experimental conditions, and, in the mixed model, it remained a small positive predictor of complex FEM likelihood. Within a restricted gestational band (33–37 weeks), modest effects are theoretically coherent. Late gestation is characterised less by abrupt functional onset and more by increasing stability, consolidation, and observability of organised responding as behavioural state cycles mature and become more differentiated (Nijhuis et al., 1982; Schneider & Prechtl, 1998).

The observed positive association between gestational age and the proportion of complex FEM patterns during stimulation, therefore, indicates that the complexity of stimulus-linked oculomotor activity increases gradually with advancing gestation. Given the restricted gestational range and the strong influence of behavioural state on behavioural

observability, modest developmental effects are consistent with models in which maturational change increases the probability of organised responding without producing sharp transitions in function (DiPietro et al., 2015).

Importantly, behavioural state remained the strongest predictor of complex responding. Relative to Quiet Sleep, the likelihood of complex FEM was substantially higher in Active Sleep, Transitional, and Quiet Awake states. This pattern supports a developmental interpretation in which maturation enhances the capacity for organised engagement, but the state continues to act as the primary gate controlling whether such behaviour is expressed at any given moment (Lecanuet et al., 2000; Nijhuis et al., 1982).

Comparison With Previous Literature

The present findings align with longstanding evidence that fetal behaviour is organised into discernible states and that responsiveness is contingent on state-related gating mechanisms (Nijhuis et al., 1982; Hunter et al., 1982). This observation addresses a recurring interpretive problem in prenatal studies, in which behavioural “non-responsiveness” has often been treated as evidence of absent perception or immaturity, without state validation. The present results demonstrate that FEM patterns systematically differ by FBS under baseline conditions, reinforcing the argument that state should be treated as a necessary interpretive context rather than an optional descriptive variable (Lecanuet & Schaal, 1996).

In fetal auditory research, most prior studies have demonstrated detection, habituation, or learning from relatively simple auditory contrasts, including vibroacoustic stimulation, maternal voice recognition, and repetition paradigms (DeCasper & Spence, 1986; Kisilevsky et al., 2000; Lecanuet & Granier-Deferre, 2017). Fewer studies have examined behavioural differentiation across complex, music-like acoustic features. The

present findings extend this literature by employing controlled contrasts designed to isolate timbre and harmonic modality while holding other stimulus properties constant, and by assessing coordinated behavioural organisation rather than relying solely on binary responsiveness. This approach complements earlier demonstrations that fetal responses vary with stimulus characteristics and developmental stage (Grant-Beuttler et al., 2011; Lecanuet & Schaal, 1996).

A central methodological contribution of this thesis is the treatment of fetal behaviour as temporally organised rather than solely count-based. Traditional approaches often summarise fetal responsiveness using aggregate frequencies within fixed response windows. However, such approaches may underestimate stimulus-linked change when behavioural responses vary in onset latency, tempo, or duration, characteristics that are typical of developing sensory–motor systems.

DTW was therefore used to quantify divergence between baseline and stimulus-evoked behavioural sequences while accommodating temporal variability. DTW is specifically designed to align sequences that unfold at different speeds or with variable timing, making it well suited to fetal behavioural data (Giorgino, 2009; Müller, 2007; Sakoe & Chiba, 1978). Across conditions, DTW distance was lowest during baseline and increased during auditory stimulation, with the largest divergence observed for string timbre and minor modality. Importantly, greater DTW divergence predicted coordinated FEM–body engagement, indicating that temporal reorganisation indexed meaningful restructuring of behavioural sequences rather than random variability.

By integrating DTW with baseline-referenced frequency and coordination measures, the present analytic framework demonstrates that temporal patterning can provide complementary information about engagement that is not captured by counts alone. This

supports the interpretation that stimulus-linked behavioural change in late gestation involves reorganisation of ongoing activity rather than merely increases in movement frequency. In this way, temporally sensitive analysis strengthens inference regarding selective, state-dependent fetal engagement with environmental stimuli (Sakoe & Chiba, 1978).

Theoretical Interpretation for Prenatal Development

The findings contribute to broader theoretical debates concerning the origins of perceptual selectivity and attentional organisation. Traditional characterisations of fetal behaviour as largely reflexive are difficult to reconcile with the consistent state-linked organisation of FEM observed under baseline conditions and with stimulus-contingent behavioural differentiation observed under controlled auditory contrasts. Instead, the results are more consistent with continuity-oriented developmental accounts in which perceptual organisation and behavioural selectivity emerge gradually as neurobehavioural systems mature and as intrauterine experience accumulates (Als et al., 2004; Lecanuet & Schaal, 1996).

Across both studies, fetal engagement was expressed behaviourally as coordinated, multimodal patterns of responding that were constrained by internal state and modulated by the structure of environmental input. Importantly, these findings do not warrant claims of adult-like perception in utero.

Rather, they support a graded account: when behavioural state and baseline activity are controlled, late-gestation fetuses show organised variation in their responses, particularly through multimodal coordination and temporal restructuring (DiPietro et al., 2015; Nijhuis et al., 1982). Within this framework, engagement reflects early forms of behavioural

organisation that precede, and potentially scaffold, postnatal attentional and perceptual systems.

Implications for Research and Practice

Several broader implications follow for both prenatal research methodology and the interpretation of fetal behaviour presented in this thesis. First, the findings reinforce that behavioural responsiveness should not be conceptualised as a binary or unitary phenomenon. Rather than reflecting simple presence or absence of perception, fetal behavioural output appears to be dynamically organised, constrained by behavioural state, and expressed through coordinated multimodal patterns.

This observation has important methodological consequences. Studies that rely solely on isolated movement counts or fixed response windows risk conflating spontaneous variability with stimulus-linked change and may therefore underestimate organised behavioural modulation. The present findings demonstrate that incorporating behavioural state validation and baseline normalisation is not merely a procedural refinement but a necessary condition for valid inference regarding fetal sensory engagement (Lecanuet & Schaal, 1996; Nijhuis et al., 1982).

Second, the analytic framework advanced in this thesis illustrates the value of treating fetal behaviour as temporally structured rather than static. By integrating refined FEM classification, multimodal coordination indices, within-subject baseline comparisons, and temporally sensitive alignment techniques, the approach moves beyond traditional detection paradigms toward a more nuanced characterisation of behavioural organisation. In particular, the use of dynamic time warping demonstrates that meaningful stimulus-linked change may manifest as reorganisation of behavioural sequences rather than increases in movement

frequency. This distinction is critical in developmental systems where response latency and tempo are inherently variable. Accordingly, temporally sensitive approaches may provide greater ecological validity when studying early sensory–motor integration (Giorgino, 2009; Sakoe & Chiba, 1978).

Third, although the present research is not designed for clinical application, the results carry interpretive relevance for applied contexts such as prenatal monitoring and developmental assessment. Strong state dependence implies that absent or attenuated behavioural responses cannot be interpreted as indicators of impaired perception without accounting for the behavioural state in which the observation occurs. Periods of reduced motor output may reflect normative quiescence rather than diminished sensory capacity. This cautions against overinterpretation of single observations and underscores the importance of repeated, state-informed assessment when behavioural indices are used in clinical or translational settings (Stone et al., 2017).

Finally, the findings contribute to a broader reconceptualisation of fetal behaviour. Rather than viewing the fetus as passively reactive to environmental input, the evidence supports an interpretation of the fetus as an actively organised system in which behavioural expression is selectively modulated by both internal regulation and external stimulation.

This perspective aligns fetal research more closely with postnatal models of attention and regulation and provides a conceptual bridge between prenatal and early infant developmental science (Als et al., 2004; DiPietro et al., 2015).

Limitations

Several limitations qualify the interpretation of the present findings and define priorities for future work. Foremost, behavioural measures provide indirect indices of

perceptual processing. Although coordinated eye and body movements can indicate organised behavioural engagement, they cannot specify the neural mechanisms or representational processes underlying discrimination. Consequently, behavioural differentiation across conditions should be interpreted conservatively as evidence of stimulus-linked behavioural modulation rather than direct evidence of cortical-level discrimination or conscious perceptual experience (DiPietro et al., 2015).

Methodological constraints inherent to ultrasound-based observation further limit inference. Eye tracking depends on fetal position, imaging angle, and visibility of ocular landmarks. Conservative exclusion criteria were necessary to protect validity but reduced usable data and may introduce selection bias if codability correlates with behavioural or anatomical factors. Similarly, categorical FEM coding necessarily discretises continuous oculomotor activity, potentially obscuring subtle gradations in movement dynamics. Although such discretisation is standard in behavioural ethology, it entails some loss of informational richness.

The use of secondary data in Study 1 introduces additional heterogeneity. Despite high imaging quality and systematic screening, retrospective standardisation of recording context, stimulus delivery, and environmental conditions cannot be assumed to be perfect. Even baseline-controlled analyses cannot eliminate all contextual variability. Study 2's smaller sample size further reduces statistical power and increases uncertainty around effect-size estimates, particularly for temporal measures.

The cross-sectional design also limits inferences about development. While associations with gestational age are suggestive of maturational trends, they do not permit direct within-individual conclusions regarding developmental trajectories. Longitudinal

designs are required to establish whether observed differences reflect true developmental progression rather than between-cohort variability.

Finally, the interpretive framework must remain ethically cautious. The absence of an observable behavioural response does not imply the absence of perception, and behavioural variability among healthy fetuses is substantial. Any application of behavioural metrics to individual-level assessment would require corroboration from physiological and longitudinal measures. Without such convergence, behavioural indicators should be regarded as research tools for understanding normative organisation rather than diagnostic markers (Hepper & Shahidullah, 1992; Van Heteren et al., 2001a).

Future Research Directions

Several research directions follow directly from these limitations and the contributions of the present thesis. Longitudinal gestational designs represent a critical next step. Repeated assessment of the same fetuses across multiple timepoints would enable within-individual modelling of changes in behavioural state organisation, FEM complexity, and stimulus-linked responsiveness. Such designs would clarify whether developmental associations observed cross-sectionally reflect genuine maturational processes and would permit investigation of individual variability in developmental trajectories (DiPietro et al., 2015).

Replication with larger samples is similarly important. Increased statistical power would stabilise effect-size estimates and enable robust testing of higher-order interactions among stimulus condition, behavioural state, and gestational age. Larger datasets would also support preregistration and cross-validation of analytic parameters, strengthen inferential transparency, and align fetal behavioural research with contemporary open-science practices.

Methodologically, future work would benefit from greater multimodal integration. Pairing behavioural measures with physiological indices such as fetal heart-rate patterning or autonomic reactivity would provide convergent evidence for engagement-related processes and reduce reliance on single-modality interpretation. Extending assessments into the postnatal period would additionally permit evaluation of predictive validity, clarifying whether prenatal behavioural organisation relates to subsequent perceptual or cognitive outcomes (Reid & Dunn, 2021).

Expanding the framework to higher-risk pregnancy cohorts offers further opportunities. Investigating whether state-dependent behavioural organisation or stimulus-linked coordination differs systematically in pregnancies affected by growth restriction, metabolic complications, or elevated prenatal stress would test the robustness and generalisability of the present findings. Although not intended as diagnostic tools, such applications could contribute to understanding how normative behavioural organisation varies across differing prenatal environments (Als et al., 2004).

Finally, future research should continue refining temporally sensitive analytic approaches. Fixed-window analyses may poorly capture behavioural systems characterised by variable latency and tempo. Techniques such as DTW and related time-series methods may therefore play an increasingly important role in quantifying developmental organisation, particularly when used in conjunction with conventional behavioural metrics (Sakoe & Chiba, 1978).

Conclusion

This thesis provides evidence that fetal behavioural organisation in late gestation is neither random nor purely reflexive, but instead structured, state-modulated, and

selectively sensitive to environmental input. Study 1 established that fetal eye movements are systematically organised across behavioural states under baseline conditions, supporting FEM as a meaningful marker of central behavioural organisation. Study 2 demonstrated that behavioural engagement can differentiate across complex auditory contrasts when assessed within a baseline-referenced and state-informed framework. Together, these findings indicate that late-gestation fetuses exhibit coordinated, multimodal behavioural modulation consistent with early forms of selective engagement.

Importantly, these behavioural patterns bear directly on core psychological constructs. Selective responding, multimodal coordination, and stimulus-contingent modulation are foundational components of perception, attention, and early information processing. Demonstrating that such an organisation is observable prior to birth situates the origins of psychological functioning within the prenatal period and extends developmental psychology beyond the traditional postnatal boundary. In this way, the thesis contributes empirical evidence to debates concerning when perceptual selectivity and attentional regulation first emerge, positioning fetal behaviour as an early expression of psychological processes rather than purely physiological activity.

Methodologically, the integration of state validation, refined behavioural coding, baseline normalisation, and temporally sensitive analyses provides a replicable template for studying prenatal sensory engagement. Importantly, this framework addresses longstanding interpretive limitations in fetal research by demonstrating that responsiveness must be evaluated relative to each fetus's own spontaneous behavioural organisation rather than inferred from isolated or absolute counts of movement. By combining behavioural state classification with within-subject contrasts and temporal

modelling, the thesis advances a more rigorous standard for distinguishing endogenous variability from stimulus-linked change.

Conceptually, the results support continuity-oriented developmental accounts in which the foundations of attentional organisation and perceptual selectivity emerge gradually before birth. Rather than marking the onset of psychological functioning, birth may represent a transition within developmental processes already underway in utero. Within this view, prenatal sensory systems are not merely maturing structurally but are functionally organising in ways that scaffold postnatal perception, attention, and learning. The presence of coordinated, state-dependent behavioural differentiation suggests that elements of selective processing, behavioural regulation, and early learning-like mechanisms are evident prior to extrauterine experience.

The thesis, therefore, contributes not only empirical findings but also a shift in how fetal behaviour is interpreted within psychological science. It encourages movement away from binary-response frameworks toward models that treat fetal behaviour as dynamically organised, temporally structured, and embedded within regulatory state systems that resemble early forms of attentional control. This reframing has implications for both theoretical models of early cognitive development and methodological standards for future prenatal research.

Overall, the findings challenge interpretations of fetal behaviour as uniformly reactive and instead portray the fetus as an actively organised system whose behavioural expression reflects the interaction of internal regulation and environmental stimulation. By situating fetal responsiveness within state-dependent and temporally structured frameworks, this thesis contributes to a more nuanced, theoretically grounded understanding of prenatal development. It establishes a foundation for future research

linking fetal behavioural organisation to postnatal outcomes. In doing so, it positions late-gestation behaviour not as an endpoint of maturation but as part of a continuous developmental trajectory, providing an essential bridge between prenatal behavioural organisation and the emergence of early perceptual, attentional, and cognitive capacities after birth.

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Appendix A

Study 1 Illustrative Poster Participant Information

Study 1:

Fetal Visual Responding

Lead Investigator: Professor **Vincent Reid**

Phone: **+64 7 838 4080** extn 9222

Ethics Committee Ref:: **2021 EXP 11521**

What Is This Study About?

We are investigating whether low levels of light can be used to project shapes that fetuses can visually perceive in the womb. This research will help us understand if and how fetuses respond to visual information before birth.

Participants Needed

- Pregnant individuals carrying a single fetus
- Between 33–36 weeks' gestation
- Healthy pregnancy & BMI of 30 or less
- Appointment lasts up to 1 hour

What Does Participation Involve?

- One 2D ultrasound scan at Waikato Hospital
- Safe light and sound stimuli
- Comfortable resting position
- Appointment lasts up to 1 hour
- Koha (vouchers) provided for participation

Data, Privacy & Ethics

- Participation is voluntary
- De-identified data stored securely
- Withdraw anytime without affecting care
- Ethics approved (2021 EXP 11521)

Need More Information?

Professor Vincent Reid

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vreid@waikato.ac.nz

Contact Professor Vincent Reid +64 7 838 4080 extn 9222

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Appendix A

Study 2 Illustrative Poster Participant Information

Study 2: Qualtrics Survey for Study Interest

HDEC Reference: 19197 | Version 2 | 02.02.2024

Auditory Perception of the Fetus

About Our Research

Our research explores how fetuses perceive music in the womb. Approved by the Southern HDEC, our studies examine responses to different musical sounds before birth.

Study Procedures

- One 2D ultrasound scan at Waikato Hospital
- Safe light and sound stimuli
- Comfortable resting position
- Appointment lasts up to 1 hour
- Koha (vouchers) provided for participation

Participants Needed

Seeking pregnant participants 35–37 weeks gestation

- *Who are carrying a single fetus*
- *1 Ultrasound session at Waikato Hospital*
- *Koha (voucher) provided for participation*

Your Data & Consent

- *1 Ultrasound scan in late pregnancy*
- *Safe, gentle sound exposure*
- *Short questionnaires*

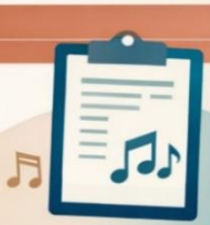
Your Data & Consent

- *Participation is voluntary*
- *Information kept confidential*
- *Withdraw any time*
- *Consent required to collect prenatal data*

Debrief Information

After your session, we'll explain findings:

- *Fetal responses to musical timbres*
- *Recognition of major vs. minor chords*
- *Insights into early auditory development*



Need More Information?

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Appendix B

Ethical Approval University of Waikato EXP 11521

Ethical Approval – Study 1

This study received ethical approval from an independent Health and Disability Ethics Committee (HDEC), which is responsible for ensuring that research involving human participants meets established ethical standards in New Zealand. Ethical approval for Study 1 was granted by the Central Health and Disability Ethics Committee.

Contact Information

Participants who have questions, concerns, or complaints about the study at any stage may contact the research team using the details below:

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Hamilton 3240
Phone: +64 7 838 4080 ext. 9397
Email: jleov@waikato.ac.nz

Independent Advocacy Support

Participants who wish to speak with someone independent of the research team may contact a Health and Disability Advocate using the following details:

Phone: 0800 555 050
Fax: 0800 2 SUPPORT (0800 2787 7678)
Email: advocacy@advocacy.org.nz
Website: https://www.advocacy.org.nz/

Māori Cultural Support

Participants requiring Māori cultural support are encouraged to speak with their whānau in the first instance. Te Puna Oranga Māori Health Services are available to provide cultural support throughout the duration of the study. A member of Te Puna Oranga can be contacted at Waikato Hospital:

Phone: 07 834 3644 Extension: 97844

Health and Disability Ethics Committee Contact

Participants may also contact the HDEC that approved this study directly:

Phone: 0800 4 ETHIC
Email: hdecs@health.govt.nz

Appendix B

Ethical Approval University of Waikato EXP 19197

THE UNIVERSITY OF WAIKATO
Te Whare Wānanga o Waikato

Ethical Approval – Study 2

Study 2 received ethical approval from the Health and Disability Ethics Committee (HDEC), an independent nationwide committee responsible for ensuring that health and disability research meets established ethical standards. The studies are registered under HDEC reference number 19197.

Contact Information

Participants may contact the lead investigator at any time if they have questions or concerns about the study:

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University of Waikato
Gate 1, Knighton Road
Hamilton 3240

Independent Advocacy Support

Participants may also contact an independent Health and Disability Advocate if they wish to speak with someone not involved in the study:

Website: https://www.advocacy.org.nz/
Email: advocacy@advocacy.org.nz

Phone: 0800 555 050
Fax: 0800 2 SUPPORT (0800 2787 7678)

Māori Cultural Support

Participants seeking Māori cultural support are encouraged to consult with their whānau in the first instance. Te Puna Oranga Māori Health Services are available throughout the duration of the study and may be contacted at Waikato Hospital:

Te Puna Oranga Māori Health Services

Phone: 07 834 3644 Extension: 97844

Health and Disability Ethics Committee Contact

Participants may also contact the HDEC directly:

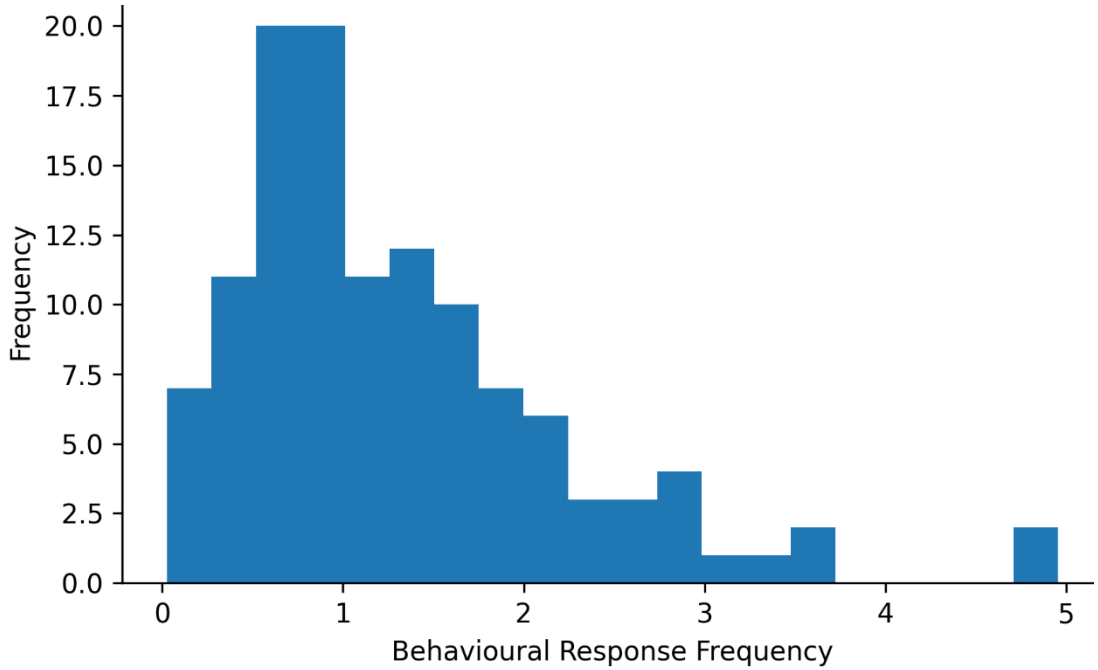
Phone: 0800 4 ETHIC
Email: hdecs@health.govt.nz

Appendix C

Supplementary Analytic Diagnostics

Figure C1

Histograms of behavioural measures used in inferential analyses.



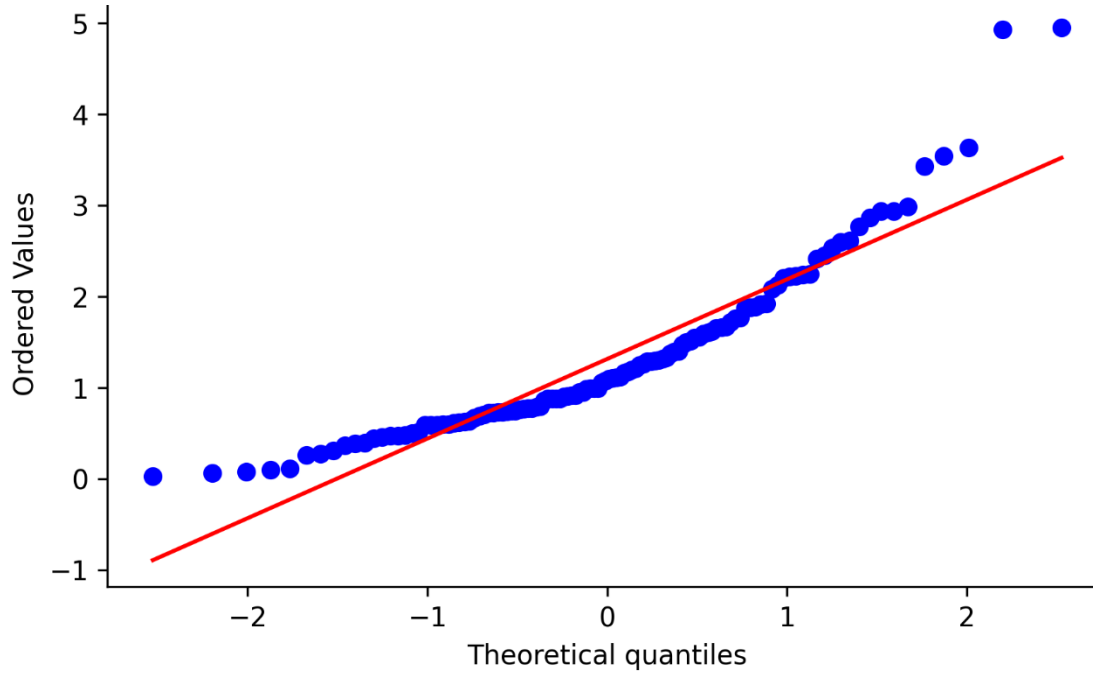
Note. Distributions indicate approximate normality across key behavioural variables, with no evidence of severe skewness or kurtosis that would violate assumptions of parametric testing.

Appendix C

Supplementary Analytic Diagnostics

Figure C2

Normal Q–Q plots for behavioural measures included in inferential analyses.



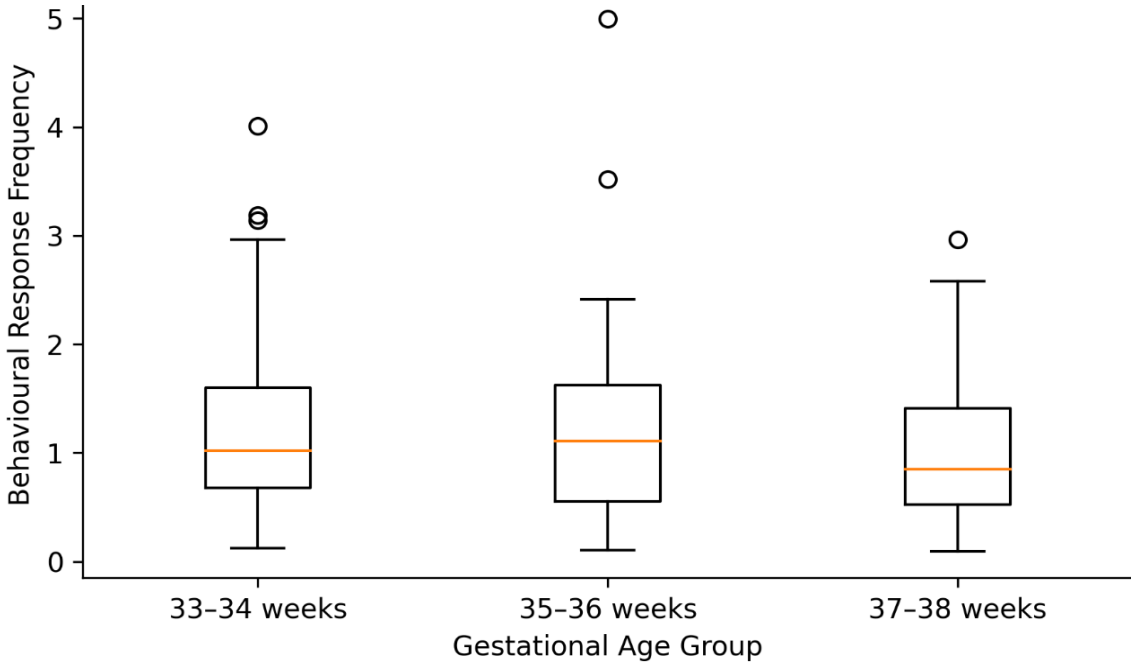
Note. Observed values closely follow the expected normal distribution, supporting the assumption of normality.

Appendix C

Supplementary Analytic Diagnostics

Figure C3

Assessment of homogeneity of variance across experimental conditions.



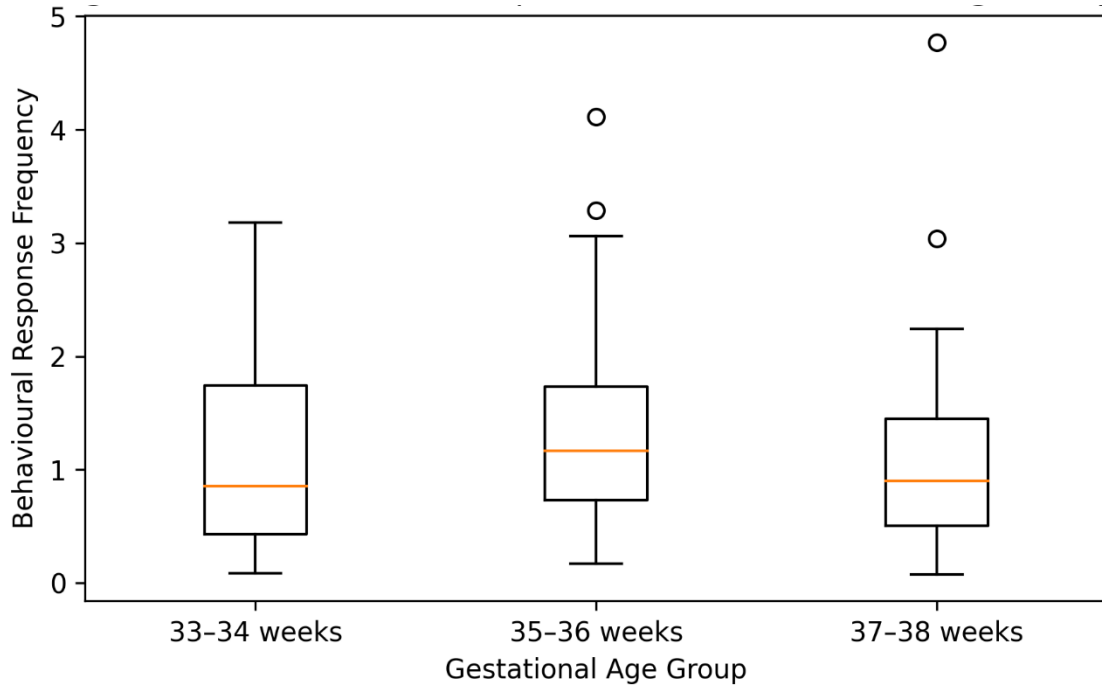
Note. Levene's test diagnostics indicate no significant violations of homogeneity of variance across conditions.

Appendix C

Supplementary Analytic Diagnostics

Figure C4

Visual inspection of variance homogeneity across behavioural measures.



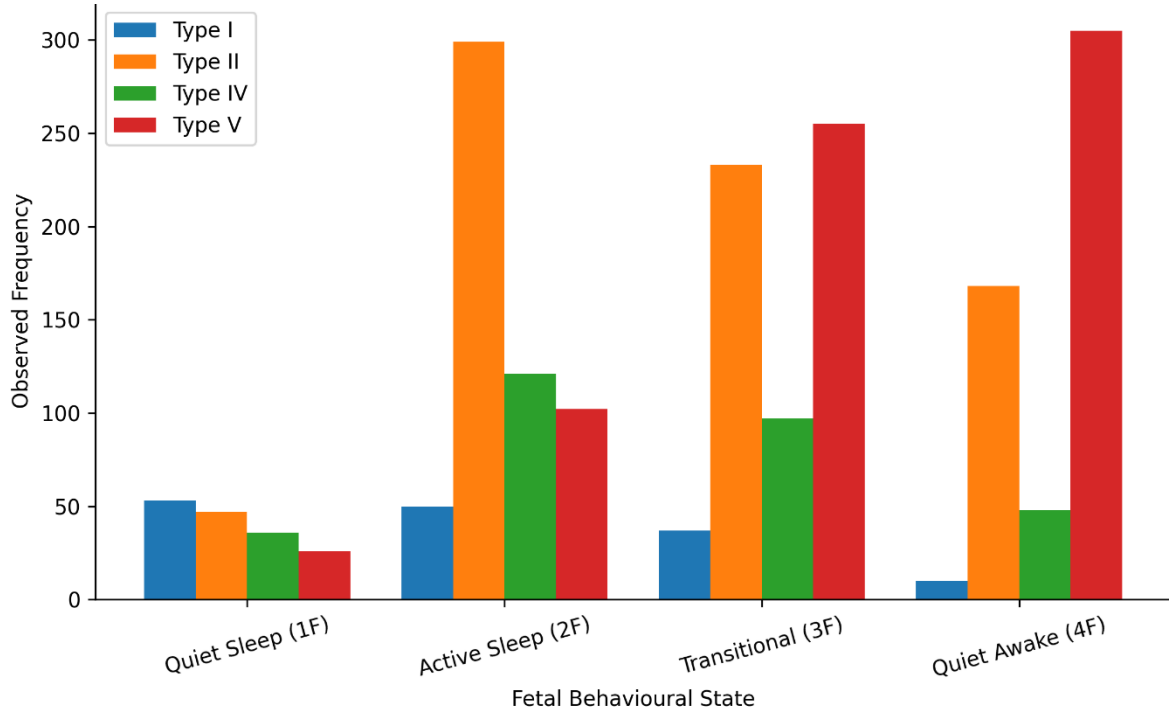
Note. Variance distributions appear comparable across experimental conditions, providing further support for the assumption of homoscedasticity.

Appendix C

Supplementary Analytic Diagnostics

Figure C5

Distribution of Refined Fetal Eye Movement (FEM) Types Across Fetal Behavioural States (FBS).



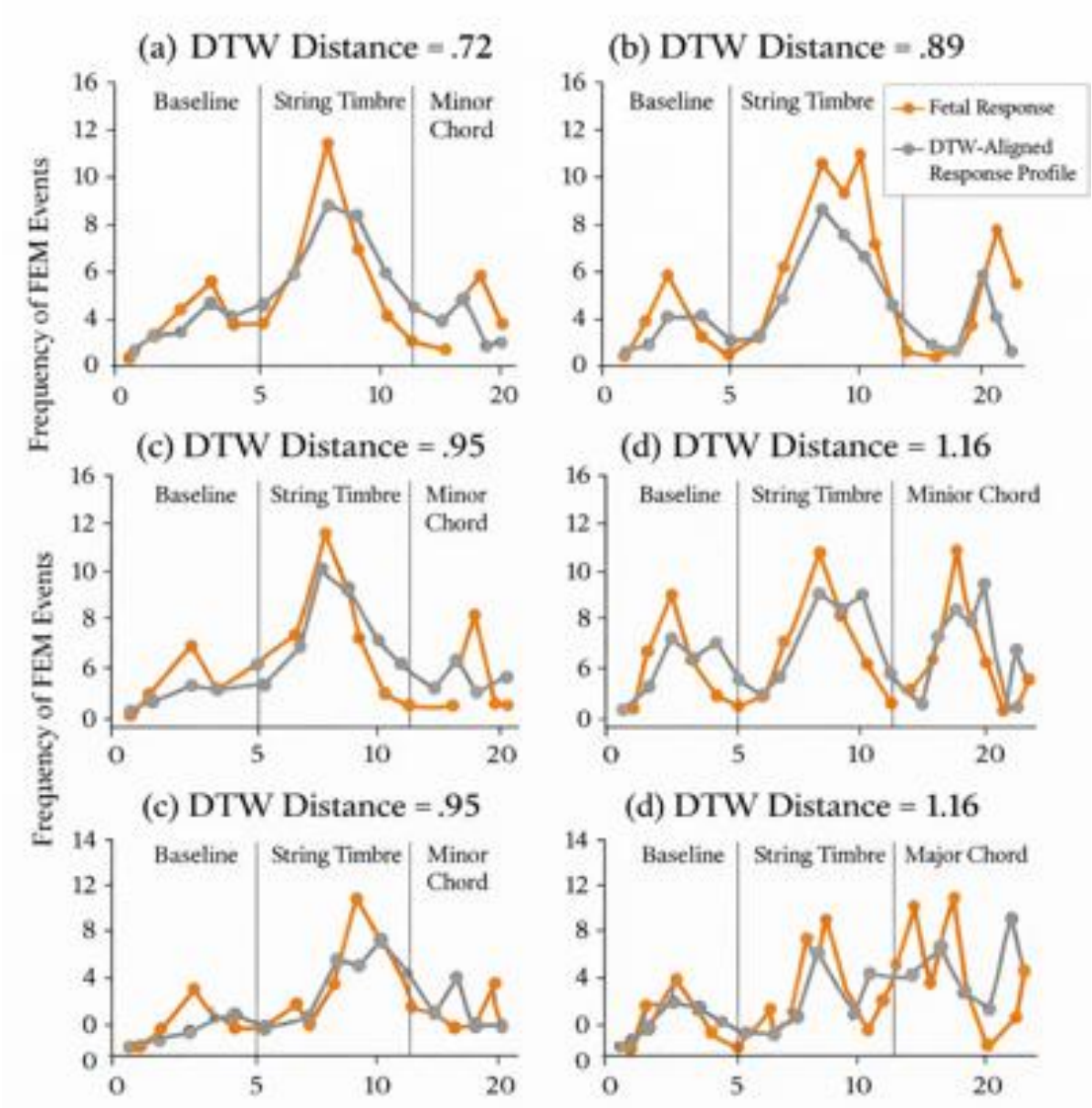
Note. Bars represent observed frequencies of FEM Types I, II, IV, and V within each fetal behavioural state. Higher-order FEMs (Types II and IV) are disproportionately represented during Active Sleep (2F), Transitional (3F), and Quiet Awake (4F) states, consistent with state-dependent sensory engagement

Appendix C

Supplementary Analytic Diagnostics

Figure C6

Illustrative examples of Dynamic Time Warping (DTW) alignment between baseline and stimulus-evoked fetal eye movement (FEM) time series across auditory conditions.



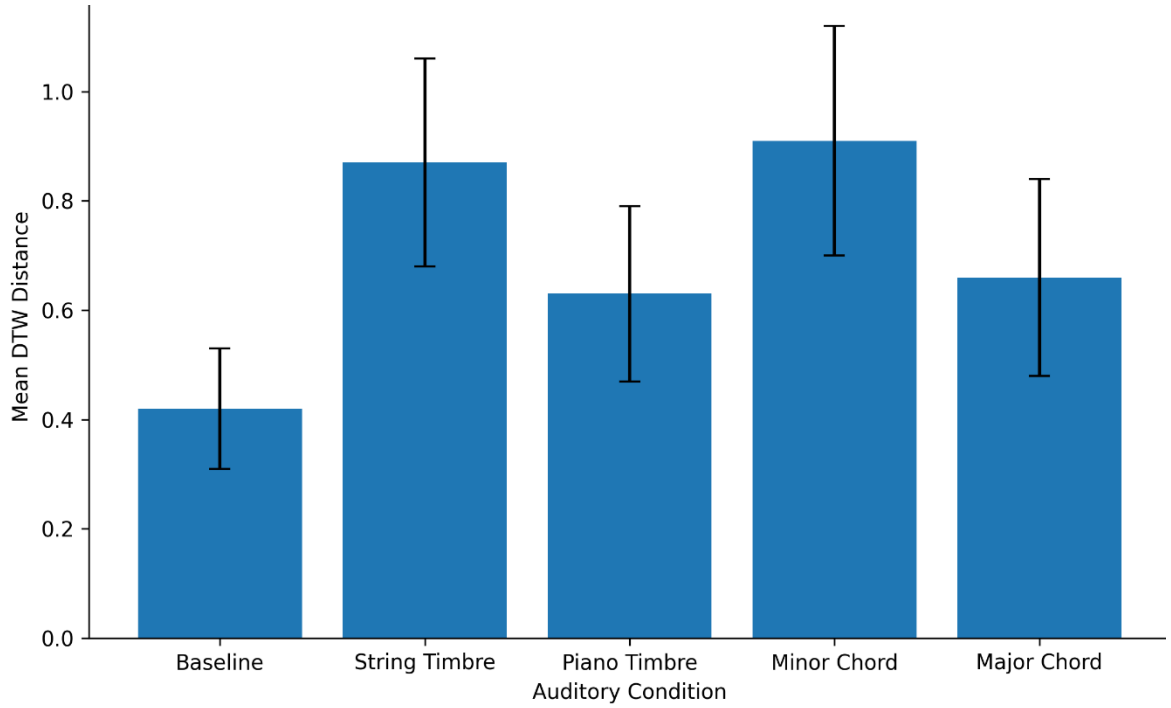
Note. Grey traces represent baseline FEM activity, and orange traces represent FEM responses during auditory stimulation. Vertical markers indicate stimulus onset and offset. DTW distance values quantify the degree of temporal reorganisation between baseline and stimulus-evoked profiles, with larger values reflecting greater divergence in the timing and structure of behavioural responses. This figure is provided for illustrative purposes to support the interpretation of DTW metrics reported in the Results.

Appendix C

Supplementary Analytic Diagnostics

Figure C7

Mean Dynamic Time Warping (DTW) Distance Between Baseline and Stimulus-Evoked Multimodal Behavioural Profiles by Auditory Condition.



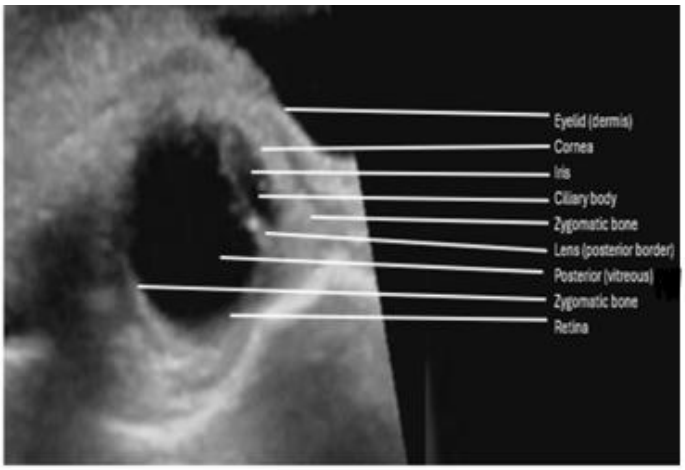
Note. Bars represent mean DTW distances for each auditory condition. Error bars indicate 95% confidence intervals. Greater DTW distances reflect increased temporal reorganisation of fetal behavioural sequences relative to baseline, with the strongest divergence observed for string timbre and minor chord conditions.

Appendix C

Supplementary Analytic Diagnostics

Figure C8

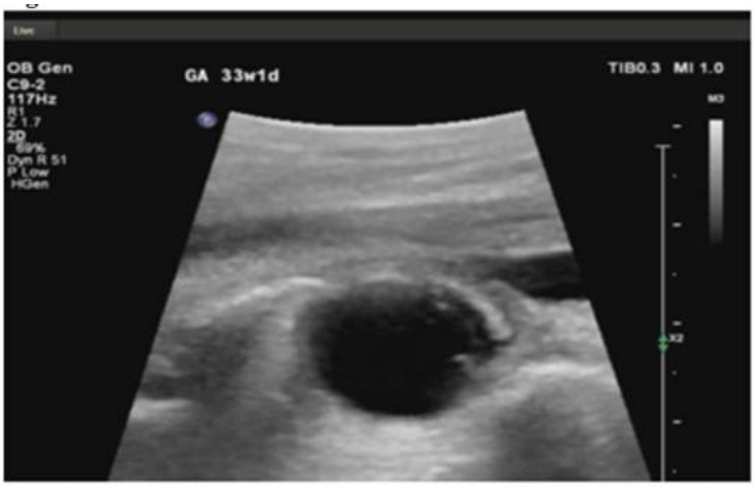
Transverse View of The Fetal Lens At 33 Weeks



Note. Anatomical view of the fetal eye

Figure C9

Transverse Plane For Imaging The Fetus



Note. Probe positioned at a right angle to maternal body's long axis, producing a horizontal cross-section of the fetus

Appendix D

Supplementary Baseline Behavioural Visualisations

Table C1

Dynamic Time Warping (DTW) Distances Between Baseline and Stimulus-Evoked Behavioural Profiles by Fetal Behavioural State (FBS)

FBS Type	DTW Distance (*SD*)	FEM–Body Coordination Index (FETA%)	Dominant Ethogram Behaviours	Interpretation of Engagement
Quiet Sleep (1F)	0.51 (0.14)	24.3%	GM, IL, HI	Limited behavioural reorganisation; low state-dependent engagement
Active Sleep (2F)	0.74 (0.18)	38.9%	FEM II–IV, GM, M, F	Moderate multimodal integration; increased stimulus sensitivity
Transitional (3F)	0.81 (0.20)	42.7%	FEM IV, GM, ST, RO	Heightened behavioural flexibility and reconfiguration
Quiet Awake (4F)	0.88 (0.22)	47.6%	FEM II–IV, GM, M, F, AF	Highest integration; sustained attentional organisation

Note. DTW distances reflect temporal dissimilarity between baseline and stimulus-linked behavioural sequences. Higher values indicate greater reorganisation of behavioural timing and structure.

Appendix D

Supplementary Baseline Behavioural Visualisations

Table C2

DTW Dissimilarity by Auditory Condition Within Fetal Behavioural States

FBS Type	Baseline	String Timbre	Piano Timbre	Minor Chord	Major Chord
Quiet Sleep (1F)	0.42	0.68	0.55	0.71	0.57
Active Sleep (2F)	0.44	0.83	0.62	0.87	0.65
Transitional (3F)	0.46	0.91	0.66	0.95	0.69
Quiet Awake (4F)	0.48	0.97	0.70	1.02	0.73

Note. Values represent mean DTW distances. Across all behavioural states, string timbre and minor-chord conditions elicited greater behavioural divergence than piano timbre and major-chord conditions.

Appendix D

Supplementary Baseline Behavioural Visualisations

Table C3

Ethogram and Fetal Eye Movement (FEM) Contributions to DTW Dissimilarity by Fetal Behavioural State

FBS Type	Primary FEM Types	Key Ethogram Behaviours	Behavioural Profile Description
Quiet Sleep (1F)	Type I–II	GM, IL	Predominantly spontaneous motor activity
Active Sleep (2F)	Type II–IV	GM, M, F, RO	Coordinated arousal-linked engagement
Transitional (3F)	Type IV	GM, ST, AF	Flexible, reconfiguring response profiles
Quiet Awake (4F)	Type II–IV	GM, M, F, RO, AF	Integrated oculomotor–somatic attention

Note. Ethogram behaviours include GM (general movements), IL (isolated limb), JM (jaw movement), Y (yawn), K (sucking), W (swallowing), SA (startle), HI (hiccup), ST (stretch), M (hand-to-mouth), F (hand-to-face), RO (head rotation), RF (head flexion), and AF (head anteflexion).

Appendix D

Supplementary Baseline Behavioural Visualisations

Table C4

Summary of DTW-Based Evidence for Complex Auditory Discrimination

Indicator	**String > Piano**	**Minor > Major**	**Interpretation**
DTW Distance	Yes	Yes	Greater temporal reorganisation for complex stimuli
FETA (%)	Yes	Yes	Stronger multimodal integration
FEM Complexity	Higher (II–IV)	Higher (IV)	Organised selective attention
Ethogram Integration	High	Highest	Coordinated behavioural profiles

Note. Converging DTW, FEM, and ethogram indicators support discriminative behavioural organisation rather than reflexive reactivity.

Appendix D

Supplementary Baseline Behavioural Visualisations

Table C5

FEM Profile Types and Associated Fetal Behavioural Characteristics (≥33 Weeks Gestation)

FEM Type	Definition	Associated Fetal Behavioural Characteristics (≥33 weeks)
Type I	Fast movement in one direction followed by a slower return movement in the opposite direction.	Common during Active Sleep (2F); accompanied by moderate body movements, stable or mildly variable heart rate, and increased responsiveness to stimulation.
Type II	Prolonged single deviation of the eyes to a medial or lateral position.	Observed during Quiet Awake (4F); associated with heightened behavioural activation, unstable heart rate, and sustained ocular orientation.
Type III	*Omitted*: insufficient definitional clarity and rarely observed in high-resolution ultrasound datasets.	Previously linked to "nystagmoid" slow oscillations, current evidence suggests poor reproducibility and unclear physiological meaning.
Type IV	Repetitive, fast, bidirectional nystagmoid movements.	Appears in Active Sleep (2F) during periods of dense REM-like activity; accompanied by irregular HR variability and frequent body movements.
Type V	Newly introduced category for FEMs that do not fit established types.	Captures atypical or transitional movements, often seen during state shifts between 1F, 2F, and 4F; associated with variable HR and mixed motor output.

Note. This table summarises five modern fetal eye movement (FEM) profile types, integrating classical observational definitions with updated evidence from high-resolution ultrasound, dynamic MRI, and contemporary behavioural-state research. Associated characteristics include body movement patterns, heart-rate variability, and gestational age patterns relevant for interpreting fetal behavioural organisation from 33 weeks onward. Representative sources include Birnholtz (1981), Nijhuis et al. (1982), Reissland et al. (2014), Donovan et al. (2020), Tamhankar and Liu (2008), Woitek et al. (2013), Pretti et al. (2022), Pramono et al. (2025), and Olson et al. (2025).

Appendix D

Supplementary Baseline Behavioural Visualisations

Table C6

Association Between FEM Types and Indicators of Sensory Engagement (≥33 Weeks of Gestation)

FEM Type	Sensory Engagement Indicator	Stimulus-Linked Responsiveness	Developmental Interpretation
Type I	Rapid orienting to changes in luminance or sound	Shows short-latency responses to visual and auditory transients; small but consistent increases in movement when stimuli are present	Reflects basic orienting response and early integration of sensory cues with motor output
Type II	Sustained ocular fixation-like behaviour	Demonstrates selective, prolonged deviation toward structured stimuli (e.g., face-like patterns, patterned light)	Indicates early selective attention and sustained sensory processing
Type III	Not included (insufficient interpretability)	Rarely observed; inconsistent stimulus-linked patterns	Lack of data introduces uncertainty and possibly suggests low developmental relevance; often artifact-related
Type IV	High-frequency scanning associated with REM-like states	Often enhanced after auditory stimulation; bursts linked to increased arousal	Reflects increased neural activation and rapid sensory-motor cycling, analogous to infant REM-related sensory gating
Type V	Mixed or transitional sensory-motor engagement	Occurs during state transitions or ambiguous responses to stimuli	Suggests developing flexibility in sensory-motor integration and incomplete state differentiation

Note. This table synthesises current evidence linking modern fetal eye movement (FEM) classifications to indicators of sensory engagement in fetuses ≥33 weeks' gestation. Type I reflects rapid orienting responses, with short-latency movements elicited by changes in luminance or sound, suggesting early sensory–motor integration. Type II corresponds to sustained ocular deviation resembling fixation-like behaviour, often observed in response to structured or face-like visual configurations, and is indicative of early selective attention processes. Type III is excluded due to insufficient interpretability and poor reproducibility in modern neuroimaging and ultrasound datasets. Type IV captures high-frequency, REM-like scanning movements that may be modulated by auditory stimulation and are associated with heightened neural activation and arousal. Type V encompasses mixed or transitional patterns occurring during behavioural state shifts, reflecting emerging flexibility in sensory–motor organisation. Representative sources include Birnholtz (1981), de Vries et al. (1982), Martin (2000), Arduini et al. (1995), Reid et al. (2017), Donovan et al. (2020), Pretti et al. (2022), Pramono et al. (2025), and Olson et al. (2025).

Appendix D

Supplementary Baseline Behavioural Visualisations

Table C7

Model Specifications for Mixed-Effects Analyses

Model	Outcome Variable	Fixed Effects	Random Effects	Distribution
Study 1 GLMM	Complex FEM	FBS, GA	Fetus ID	Binomial
Study 2 GLMM	FETA	Condition, GA	Fetus ID	Binomial
DTW LMM	DTW distance	Condition, GA	Fetus ID	Gaussian
Integrative GLMM	FETA	DTW, GA	Fetus ID	Binomial

Note. FEM = fetal eye movements; FETA = coordinated fetal eye movement–body activity; FBS = fetal behavioural state; GA = gestational age. All models included a random intercept for fetus identity.

Table C8

Summary of Model Diagnostics and Assumption Checks

Model	Category Normality	Homoscedasticity	Convergence
Study 1 GLMM	Not applicable	Acceptable	Yes
Study 2 GLMM	Not applicable	Acceptable	Yes
DTW LMM	Acceptable	Acceptable	Yes
Integrative GLMM	Not applicable	Acceptable	Yes

Note. Residual normality was assessed only for linear mixed-effects models. Diagnostic plots, including Q–Q plots and residuals-versus-fitted plots, are provided in Appendix Figures C5–C8.

Appendix E

Glossary of Operational and Conceptual Definitions

The following glossary provides operational and conceptual definitions of key constructs used throughout this thesis. Definitions reflect the specific measurement framework and analytic procedures adopted in Studies 1 and 2 and are intended to enhance interpretive clarity and reproducibility.

Arousal Regulation
The organisation and modulation of behavioural activation levels across fetal behavioural states, influencing sensory gating, motor availability, and responsiveness to environmental stimulation.

Auditory Discrimination
The capacity to behaviourally differentiate between distinct acoustic properties, such as timbre or harmonic modality, is reflected in systematic variation in fetal eye movements, fetal body movements, or coordinated behavioural responses across stimulus conditions.

Baseline Behaviour
Spontaneous fetal behavioural activity observed during periods without experimental stimulation. Baseline behaviour provides the reference framework against which stimulus-evoked changes are evaluated.

Behavioural Complexity
The degree of coordination, variability, and structured patterning observed across fetal eye and body movements is interpreted as reflecting maturation of sensorimotor integration and central nervous system development.

Behavioural Coordination
The temporal coupling of fetal eye movements and fetal body movements within defined observation windows, particularly during stimulus presentation.

Behavioural Organisation
The structured coordination and temporal patterning of fetal eye movements, body movements, and behavioural state reflect the maturation of central nervous system regulation and sensorimotor integration.

Central Nervous System (CNS) Maturation
Progressive structural and functional development of neural circuits supporting sensorimotor integration, behavioural state organisation, and stimulus responsiveness across gestation.

Continuity Model of Development
The theoretical perspective that psychological processes emerge prenatally and continue across the birth transition rather than beginning at birth, positioning fetal behaviour within an ongoing developmental trajectory.

Coordinated Engagement (FETA)
Fetal Evoked Transitory Arousal. A temporally defined period during which fetal eye

movements and fetal body movements co-occur in a structured manner following stimulus onset, operationalised as a binary indicator of multimodal behavioural coordination.

Discriminative Behavioural Modulation
Condition-specific variation in behavioural response patterns that differ systematically between stimulus types, suggesting selective processing rather than generalised arousal.

Dynamic Time Warping (DTW)
A time-series analytic method used to quantify similarity or divergence between baseline and stimulus-evoked behavioural sequences. Larger DTW distances indicate greater temporal reorganisation relative to baseline behavioural organisation.

Effect Size
A quantitative measure of the magnitude of an observed effect (e.g., Cramer's V, Cohen's d), independent of statistical significance.

Fetal Behavioural State (FBS)
A higher-order organisational construct inferred from the integrated patterning of fetal eye movements and fetal body movements across sustained observation windows. States 1F–4F correspond broadly to quiet sleep, active sleep, transitional, and quiet awake behavioural profiles.

Fetal Body Movements (FBM)
Observable motor behaviours coded from ultrasound, including general movements, startles, isolated limb movements, head movements, and directed actions such as hand-to-mouth contact. FBM serves as an indicator of spontaneous motor activity and stimulus-linked modulation.

Fetal Eye Movements (FEM)
Observable displacements of the fetal lens within the orbital socket are classified into operationally defined categories. FEM are treated as indices of state-dependent sensory readiness and central oculomotor organisation.

Generalised Linear Mixed-Effects Model (GLMM)
A statistical modelling framework that incorporates both fixed effects and random effects to account for repeated observations within fetuses while estimating condition-related behavioural effects.

Gestational Age (GA)
Fetal age is calculated in days or weeks since conception and is treated analytically as a continuous developmental predictor variable.

Harmonic Modality
A musical property determined by intervallic structure, particularly the third (e.g., major versus minor chord), was examined in Study 2 to assess discriminative behavioural modulation to complex acoustic features.

Multimodal Behavioural Profile
The integrated time-series representation of fetal eye movements, fetal body movements, and behavioural state across baseline or stimulus epochs.

Random Intercept
A modelling parameter in mixed-effects analyses that allows baseline behavioural levels to vary across individual fetuses, accounting for the non-independence of repeated measures.

Selective Sensory Engagement
Stimulus-linked behavioural modulation that exceeds spontaneous baseline variability and varies as a function of behavioural state, gestational age, or stimulus characteristics. Selective engagement implies organised processing rather than non-specific arousal.

Sensorimotor Integration
The functional coordination between sensory input and motor output systems is reflected behaviourally in structured, state-dependent responses to environmental stimulation.

Sensory Gating
Modulation of sensory responsiveness as a function of behavioural state determines whether and how stimuli influence motor expression.

Spontaneous Behaviour (SB)
Endogenously generated fetal motor and ocular activity occurs without identifiable external stimulation. SB reflects intrinsic neural self-organisation and developmental maturation.

State-Dependent Processing
The principle that sensory responsiveness and motor expression vary as a function of behavioural state, such that identical stimuli may elicit different behavioural outcomes depending on the fetus's prevailing organisational state.

State Stability
The duration and consistency with which a fetus remains in a defined behavioural state reflect the maturation of central regulatory systems.

Stimulus-Evoked Behaviour (SEB)
Behaviour occurring during or immediately following experimental stimulation that demonstrates measurable deviation from baseline spontaneous organisation.

Temporal Reorganisation
A measurable change in the timing, sequencing, or coordination of behavioural events between baseline and stimulus conditions, quantified using Dynamic Time Warping.

Timbre
The perceptual quality of a sound that distinguishes different instruments playing the same note at identical pitch and amplitude. In Study 2, timbre was operationalised through controlled comparison of string and piano tones.

Transnatal Continuity
The principle that prenatal sensory exposure can influence postnatal perception and preference, reflecting continuity of learning across the birth transition.

Within-Subject Comparison
An analytical approach that compares baseline and stimulus periods within the same fetus to control for inter-individual variability.