



An embodied approach to fetal and newborn perceptual and sensorimotor development

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ABSTRACT

The embodied approach argues that interaction with the environment plays a crucial role in brain development and that the presence of sensory effects generated by movements is fundamental. The movement of the fetus is initially random. Then, the repeated execution of the movement creates a link between it and its sensory effects, allowing the selection of movements that produce expected sensations. During fetal life, the brain develops from a transitory fetal circuit to the permanent cortical circuit, which completes development after birth. Accordingly, this process must concern the interaction of the fetus with the intrauterine environment and of the newborn with the new aerial environment, which provides a new sensory stimulation, light. The goal of the present review is to provide suggestions for neuroscientific research capable of shedding light on brain development process by describing from a functional point of view the relationship between the motor and sensory abilities of fetuses and newborns and the increasing complexity of their interaction with objects in the womb and outside of it.

1. Introduction

The purpose of this narrative review is to use an embodied approach to suggest how sensorimotor and perceptual abilities develop in humans during prenatal and perinatal life. This perspective agrees with what Marshall and colleagues (Marshall et al., 2021) claim regarding the deep connections between embodiment and development. These authors underline that all living beings share embodiment, since all living beings have a body, and the body does not exist separately from the actions and activities of the individual. As animal bodies evolved, so did their ability to act, becoming more complex and adaptable because of the development of nervous systems. Specifically, the enactivist approach proposes that the world experienced by an organism depends on its own embodied activity, and that this interaction determines a structural coupling between organism and environment, rejecting conceptions that strongly demarcate minds from bodies and environments, as well as the traditional input–output processing model of the mind (Marshall, 2016; Varela et al., 2016). Consequently, a fundamental premise of embodiment is that action is not the “output” of cognitive processing, and that the organism is not a passive recipient of “information” with pre-specified meaning. Instead, the organism is considered active, and its processes are anticipatory and future-oriented (Marshall et al., 2021). A related key concept on which the viewpoint discussed in the present article is based on, is that of refference, defined by Jékely and

colleagues (Jékely et al., 2021) as “any effect on an organism’s sensory mechanisms that is due to the organism’s own actions”. These authors apply to early nervous system evolution the general principle that self-initiated actions evoke sensory change, suggesting how the structure, morphology, and sensory systems of the body have coevolved to use refferent sensing. Hence, the body and brain are not assembled according to a simple genetic blueprint. Self-induced action is considered a central ingredient for perception, and behavior acts as a device that controls perceptual input (i.e., operant behaviour) (Brembs, 2009). In fact, since self-initiated actions are associated with sensory effects, it is possible to anticipate and make use of these effects (refference principle) (Jékely et al., 2021). Furthermore, many species employ motion to trigger environmental stimuli that they would not otherwise experience. As an example, bacteria such as *Escherichia coli* use motility to assess the presence of chemical gradient (Adler, 1965). Refference also includes self-initiated alterations in bodily postures and responses to applied force, such as during active touch (Turvey & Fonseca, 2014).

Such insights have great implications for developmental psychology, whose central question is: How do children come to know about the world, and what are the origins of knowledge? The previous dominant model was deterministic, influenced by models of embryological development and gene expression (Gottlieb, 1976, 1998). The brain’s anatomical maturation was believed to facilitate the functional advances that were exhibited in behavior, suggesting a unidirectional link

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between brain and behavioral development. Rather, the new neurobiological perspective emphasizes the reciprocity and interdependence of the relationship between brain and behavioral development (Stiles, 2009). Critically, in the second trimester of gestation, up to 50 % of the cortical neurons are subplate neurons, a unique class of cells seen in the developing cerebral cortex that constitute one of the earliest functional cortical circuits (Kanold, 2009; Ohtaka-Maruyama, 2020). The human subplate develops between weeks 13 and 15 of pregnancy, continues to be the largest compartment of the neo cortical anlage between weeks 15 and 30, and then gradually begins to disappear in the final stages of pregnancy and the early postnatal period (Judaš et al., 2013). The subplate contains numerous neurons of various morphological types and molecular phenotypes. Various afferent fibers sequentially grow into the subplate, establish temporary synaptic circuits, and “wait” in the subplate for several months before relocating into their final target, the cortical plate (Kostovic & Goldman-Rakic, 1983; Kostovic & Rakic, 1990; Krmpotić-Nemanić et al., 1983). Short corticocortical connections grow relatively slowly, lasting at least a year after birth, whereas long corticocortical connections start to form in the early prenatal period (Kostović et al., 2014; Vasung et al., 2011). Hadders-Algra (Hadders-Algra, 2018) reviewed literature reporting that the most significant developmental changes in the brain occur during the second half of gestation and the first three months post-term in the cortical subplate and cerebellum. Furthermore, disruption of the development of the subplate is associated with a high risk of developing cerebral palsy, cognitive impairment and psychiatric disorders, including ASD and ADHD. Brain development does not only imply the generation of neurons and connections, but it also involves regressive phenomena. Animal experiments indicated that apoptosis, i.e. neuronal death, is the result of interaction between endogenously programmed processes and chemical and electrical signals induced by experience (Lossi & Merighi, 2003). In the cerebral cortex apoptosis is very active in the third trimester of gestation (Rabinowicz et al., 1996). Well-known examples are the pruning and tuning of the corpus callosum and that of the corticospinal tract. This reorganization is activity driven and use dependent (Eyre, 2007).

Therefore, according to the embodied enactivist approach, the transition from the transitory fetal circuit to the immature but progressively developing permanent cortical circuit must relate with the interaction of the fetus with the intrauterine environment. To provide suggestions for neuroscientific research that can shed light on the mechanisms underlying this process, the present review describes from a functional point of view the relationship between the development of motor and sensory abilities of the fetuses and newborns and the increasing complexity of their interaction with objects in the womb and outside of it. It is also suggested that refference (Jékely et al., 2021) may play a crucial role, allowing the plastic and maturational processes to manifest sensorimotor binding. The article also describes the necessity for the newborn to adapt to the extrauterine environment in which the stimuli affect all the sensory organs simultaneously and directly, and the movements are performed in an aerial rather than an aquatic medium. Additionally, vision, a newly available sense at birth, must be integrated with the sensorimotor knowledge gained from interactions with the intrauterine environment to enable actions and perceptions in the new environment.

2. Before birth

To understand the type of interaction the fetus probably has with objects in the womb, this section separately describes the sensory environment and the functional development of sensory skills, the functional development of motor skills, and how refference may give rise to the sensorimotor binding. Particularly for sensory development, this review seeks also to highlight the experimental difficulties in investigating the actual ability of the fetus to perceive stimuli. In fact, only the presence of a stimulus-evoked change in behaviour or

physiological functions (e.g., heart rate, brain activity) guarantees that the administered stimulus has been processed. Because of this, it is exceedingly challenging to get a good picture of the sensory data that the fetus has access to, an information essential for studying its interaction with the intrauterine environment.

2.1. The sensory

Fetuses are in conditions comparable to neutral floating until the 21-22nd gestation week (GA). As astronauts in the zero-gravity world, for them there are no “ups” or “downs”. Only after 26 GA the apparent weight of the fetus is 60–80 % of the actual weight (Sekulić et al., 2005). The senses are silent during the first weeks of gestation, and later they become functional in a specific and invariant sequence, tactile > vestibular > chemical > auditory > visual, a common rule of the development of the sensory systems of birds and mammals (Gottlieb, 1971). The various sensory modalities therefore have very distinct developmental histories at birth, as the tactile and vestibular systems that developed earlier have accumulated much more experience than the auditory system that developed later. It has been proposed that the differential timing onset allows earlier-developing sensory systems to develop without competition or interference from later-developing sensory systems (Turkewitz & Kenny, 1985). Indeed, a series of studies on quail chicks suggested that premature stimulation of a later developing sensory system may alter the functioning of earlier ones, indicating that the development of early sensory organization is plastic and experience-dependent, and also highlighting the importance of normal developmental limitation of sensory input. As an example, chicks typically show a naïve auditory preference for their species-specific maternal call within 24 to 48 h after hatching. However, when the hatchlings are stimulated with patterned light during the 24–36 h before hatching, they no longer exhibit this preference (Lickliter, 1990). In another study, chicks exposed to augmented prenatal tactile and vestibular stimulation continued to respond to maternal auditory cues into later stages of postnatal development and failed to demonstrate responsiveness to maternal visual cues in the days following hatching. However, this augmented prenatal stimulation did not appear to affect prenatal auditory learning of an individual maternal call, indicating a selective pattern of influence between the sensory modalities (Carlsen & Lickliter, 1999). Taken together, this animal-based research implies that alterations of perinatal sensory stimulation (i.e., in the timing, in the amount of stimulation provided or denied, and in the type of sensory stimulation) may influence early perceptual and behavioral development (Lickliter, 2000). The restricted and buffered developmental context of the uterus, along with the fetus’s limited sensory capacities (due to the sequential onset of sensory system function prenatally), combine to effectively limit and regulate the relative quantity, kind, and timing of sensory stimulation available during the prenatal period. This control, unfortunately, is totally lacking in the premature baby in the NICU who receives decreased amounts of tactile and vestibular stimulation from maternal motion normally available in utero, and substantially increased amounts of other types of stimulation which are not present in the intrauterine environment (e.g., unfiltered auditory stimulation and patterned visual stimulation) (Lickliter, 2011). Studies have suggested that this atypical sensory environment may have effects on the developing premature brain (Gressens et al., 2002).

2.1.1. Touch

The somesthetic system is the very first sense to form, developing according to a cephalo-caudal pattern. At 8 GA, neuronal free-ending receptors are found in the epithelium of the mouth and the dermis of the perioral region. By 11 GA, tactile receptors are found on the face, palms, and soles, by the 15 GA on the trunk and proximal zones of arms and legs, and by the 20 GA on the entire skin (Lecanuet & Schaal, 2002).

The placenta, umbilical cord, amniotic fluid, and the surface of the uterus all contact the fetus continuously, and fetus can touch its body

passively or actively as self-initiated movements emerge. The sound generates vibrations that are transmitted to the amniotic fluid and from it to the body/head of the fetus. Thus, it is not easy to distinguish the contribution of the somatosensory and acoustic systems when experimental studies use so-called vibroacoustic stimulations. We decided to deal with these results in the paragraph dedicated to sound, and here to deal only with the data relating to the exploration of responses to direct touch. This type of study is only possible in two ways: indirectly, by verifying the effects of pressure on the maternal womb, and directly, by touching the body of the fetus.

During fetal development, the mother's movement when standing, walking, or dancing provides a unique source of somatosensory and vestibular stimulation (Bellieni et al., 2003). Furthermore, it is reasonable to believe that a mother's touch of her belly during pregnancy exerts a slight pressure, and as a result, the abdomen, including the uterine environment move and thus, passively stimulate and touch the fetus. Very few are the studies investigating this topic, showing that fetuses at 21–33 GA increased their arm, mouth, and head movements when the mother touched the abdomen compared to when the mother just spoke or did nothing (Marx & Nagy, 2015), and that differential responses to the touch are dependent on the gestational age. Specifically, fetuses in the 3rd trimester touched the wall of the uterus for a significantly longer time than fetuses in the 2nd trimester (Marx & Nagy, 2017).

The study of the effect of the direct stimulation of the body of the fetus was only possible until the middle of the last century. Hooker, an anatomist at the University of Pittsburgh, took advantage of the few moments of vitality of aborted fetuses, following a therapeutic hysterectomy, to observe them, touch them with a hair on the face, body, arms and legs, and film their movements. Over the course of about thirty years, Hooker observed more than 150 fetuses and premature infants in this way. The project produced over forty articles and a nine-minute medical film and contributed information and photographic images to numerous scientific publications. After the abortion debate and the development of biomedical ethics in the 1960s and 1970s, this kind of research was abandoned (Wilson, 2014). Thanks to these studies, however, it was possible to establish the presence of a motor reflex to touch already at 7–8 GA, that is, after stroking the perioral region, contraction of the neck muscles on the side opposite the stimulation has been observed, and that during the following weeks of development, sensitivity extends along an anteroposterior axis to the entire body and is complete by 14 GA (Hooker, 1952).

2.1.2. Flavor

According to physiological and pharmacokinetic studies of drugs, most molecules can cross the placenta, some by passive diffusion and others by facilitated diffusion (Syme et al., 2004). However, to date, only one study, by using a sensory analysis of amniotic fluid, has demonstrated the actual transplacental transfer of flavor molecules. Pregnant women were asked to ingest either capsules containing the essential oil of garlic or placebo capsules. About 45 min later, samples of amniotic fluid were obtained during the routine amniocentesis procedure and then evaluated by a sensory panel of adults (Mennella et al., 1995).

Immunohistochemical studies indicate that taste buds develop anatomically at 8 GA, and that at the same time the olfactory cells also appear (Witt & Reutter, 1998). Olfactory sensory neurons are active from 24 GA (Witt, 2020). Starting from 11 GA the fetus swallows amniotic fluid. This activity is thought to contribute to the regulation and homeostasis of amniotic fluid volume, intrauterine fluid acquisition and recirculation, and fetal growth. From 10 GA, the so-called respiratory movements are present, irregular in frequency and amplitude, which contribute to the development of the lungs (Koo & Rajaei, 2014). These behaviors allow substances present in the amniotic fluid to reach taste and smell receptors.

An indirect approach is typically used to test the functional maturity of the fetus's gustatory/olfactory system. This involves testing newborns

with chemostimuli that they were likely exposed to during pregnancy in the hours or days after delivery (Spahn et al., 2019). For example, if their mothers had consumed at least four meals containing garlic each week throughout the final month of their pregnancy, newborns aged 15 to 28 h did not exhibit an adverse response to the smell of garlic (i.e., the time the baby spent with its head facing the garlic was similar to that facing a control odor) (Hepper, 1995), or if mothers consumed anise-flavored sweets in the last 2 weeks of pregnancy, neonates up to 4 days of age preferred the anise odorant, compared to controls, according to their facial responses and head orientation (Schaal et al., 2000). These findings suggest the ability to detect flavor at least during the last trimester of pregnancy, and the presence of stable, long-term retention of these experiences. There are, however, no functional studies on humans that allow us to know whether fetuses perceive chemosensory stimuli before the last trimester of pregnancy. To know this, it would be necessary visualizing the spontaneous, immediate responses of surgically prepared fetuses to flavors in utero, an approach used in various nonhuman models (Smotherman et al., 1991).

The first direct evidence of human fetal responsiveness to flavors transferred via maternal consumption was recently published (Ustun et al., 2022). The study coded 4D ultrasound scans (4DUS; see later for a description of the technique) to examine how fetuses from 32 to 36 weeks of gestational age react to different flavors transferred to the fetal environment by maternal ingestion. The authors compared the facial movements and facial gestalts from three groups of fetuses exposed to either carrot flavor, kale flavor, or no flavor, ingested in capsules by their mothers. Results showed more laughter-face gestalts when exposed to a carrot flavor and more cry-face gestalts when experiencing a kale flavor, which are facial movements similar to those of newborns exposed to comparable flavors (Ustun et al., 2022). These results also provide important information regarding transplacental kinetics of flavorants ingested by mothers, showing that the ingestion of only 400 mg of substance is sufficient to reach fetal chemoreceptors within a relatively short time. In around 30 min the flavor content of the capsules undergoes digestion, absorption into the mothers' bloodstream, metabolism and circulation through the placenta and fetus, collection in the amniotic fluid, and fetal chemoreceptors.

2.1.3. Sound

Experimental evidence gathered primarily from pregnant sheep (Gerhardt et al., 1990) delineated the acoustic nature of the intrauterine environment, subsequently confirmed also in humans (Richards et al., 1992). Specifically, sound energy in the amniotic fluid stimulates fetal hearing via a bone conduction pathway rather than through the external and middle ear systems (Gerhardt & Abrams, 1996), as it happens in divers underwater (Hollien & Feinstein, 1975). Bone conduction stimulation produces a symmetrical input to the central auditory system, thus the opportunity to localize sounds is probably not available to the fetus (Dirks, 1995), unless they rely on the localization of tactile information generated by the waves of amniotic fluid carrying the stimulus. Sounds generated inside the mother and present in the uterus are associated with maternal respiratory, cardiovascular, intestinal activity, and physical movements. These sounds, mainly at low frequency (<100 Hz) and at a sound pressure level of 90 dB, provide a background above which externally generated sounds emerge. Furthermore, external stimuli are shaped by the tissues and fluids of pregnancy before reaching the fetal head, which act as a low-pass filter that rejects high-frequency energy (Gerhardt & Abrams, 1996). Less than 5 dB of attenuation occurs for frequencies below 500 Hz of low-frequency sound energy, which easily reaches the fetal head, instead, up to 20 to 30 dB of attenuation occurs for higher frequencies. Complex sounds such as the human voice or music are less attenuated than pure tones (Granier-Deferre et al., 2011). Furthermore, voice identification, prosody, and certain phonetic characteristics are retained in speech recorded intra-amniotically and can be recognized by adults (Querleu et al., 1989). Sound energy is mildly attenuated for frequencies below 250 Hz (10 to 20 dB) and

greatly attenuated for frequencies between 500 and 2,000 Hz (40 to 50 dB) when they pass through the bones of the skull. Therefore, a fetus in utero is likely unable to perceive acoustic energy at frequencies higher than 500 Hz, but it may easily detect lower frequency sound energy (Gerhardt & Abrams, 1996).

Morphological structures of the peripheral auditory system essential for hearing develop by 20 GA (Pujol et al., 1991). The auditory nerve is well developed between 26 and 29 GA, one to two weeks before the brainstem and central auditory pathways are myelinated (Moore et al., 1995) (for a recent review on auditory foetal development see Ghio et al. (Ghio et al., 2021)). Techniques that can be used to test auditory function directly—like evoked otoacoustic emissions—cannot be utilized during the fetal stage. Behavioral responses to auditory stimuli are the only direct technique to study the functional development of the fetal auditory system. Birnholz and Benacerraf (Birnholz & Benacerraf, 1983) used high-resolution ultrasound imaging for observing eye-blink responses (auro-palpebral reflex) to a vibroacoustic noise source with output intensity of about 110-dB applied to the maternal abdomen directly overlying a fetal ear, in 236 fetuses between 16 and 32 GA. They found that responses occurred between the 24 and 25 GA and were present consistently after 28 GA (Birnholz & Benacerraf, 1983). Hepper and Shahidullah (Hepper & Shahidullah, 1994), using ultrasound recording, reported that the 27 GA fetuses showed motor responses to 250 Hz and 500 Hz tone frequency, and, using a habituation–dishabituation procedure, showed that at 35 GA they can discriminate between both sounds (Shahidullah & Hepper, 1994).

In addition to behavioral data, fetal magnetic brain responses to auditory stimuli between 28 and 34 GA were reported in several magnetoencephalography (MEG) studies (Eswaran, Preissl, et al., 2002; Zappasodi et al., 2001). MEG measures the magnetic field associated with electrical activity, and it is a highly ideal technique for fetal brains recording since it is noninvasive, it does not require to attach electrodes to the skin, and it is unaffected by changes in tissue boundaries. However, the relatively low success often reported by various studies may be attributed not only to the immaturity of the fetal brain but also to several technical factors, including the distance between the fetal head and the sensors, movement of the fetal head during data acquisition, sub-optimal placement of the sensors relative to the abdominal region containing most of the evoked signal (Eswaran et al., 2005). In fetal MEG recordings the magnetic sensors are distributed over a concave array whose shape is designed to match the maternal abdomen (Sheridana et al., 2010). Evoked responses require development of the auditory nerve and myelination of the brainstem and central auditory pathways, so are not detected before 28 GA (Moore et al., 1995). Draganova and colleagues (Draganova et al., 2007) investigated the presence of mismatch negativity (MMN) response. This component relates to the difference in waveform obtained by subtracting the evoked response to the standard tone from the deviant tone and reflects the presence of a discriminative capability. The results showed that discriminative brain responses to sound changes can be detected at least as early as 28 GA and that the detection rate did not change over GA.

Fetuses are supposed to perceive speech sounds since they detect sound energy frequencies lower than 500 Hz (the fundamental frequency range for voiced speech in an adult male is 85–155 Hz, in adult female is 165–255 Hz). A special case is represented by the maternal voice, as it undergoes very little if any attenuation thanks to internal transmission (Granier-Deferre et al., 2011). The particular nature of mother's voice is reflected by results of heart rate measurements showing that fetuses at 36 GA evidenced no ability to discriminate between their mother's and a stranger's voice played to them via a loudspeaker on the abdomen but did discriminate between their mother's voice when played to them by a loudspeaker on the abdomen and the mother's voice produced by her speaking (Hepper et al., 1993). The fact that the maternal voice is perhaps the most salient of all auditory stimuli in the intrauterine environment can probably explain the evidence that near-term fetuses can discriminate, by showing distinct heart rate

responses, between native and non-native languages (Kisilevsky et al., 2009), and between tape recordings of a rhyme previously repeatedly recited by their mother and a control rhyme, when the two rhymes were read by a female stranger's voice (DeCasper et al., 1994).

2.1.4. Light

Regarding the visual system, rods and future cones can be found by the end of the 12 GA, but the development of photoreceptor cells is not completed before birth with the macula not being fully developed until a few months after birth (Alabduljalil et al., 2019). The immature retina exhibits patterns of spontaneous activity, showing highly correlated bursts of action potentials (retinal waves) that are transmitted to the entire developing visual system, thereby providing a robust source of activity before the onset of visual experience (Arroyo & Feller, 2016; Khazipov & Luhmann, 2006). The eyelids typically can open around 20–22 GA, reducing the potential attenuation of the light before it reaches the fetal retina (Fulford et al., 2003).

It is necessary to point out that the amount of light inside the uterus is very low. A study conducted on pregnant sheep (term 147 days), placed in a study cage outdoors, showed that light detected inside the uterus increased with gestational age from 2 lx at 40 days to 51.1 lx at 142 days, corresponding to 0.2 % and 5.4 % of the amount of light detected at the maternal flank (Parraguez et al., 1998). Given that the pregnant sheep is often taken as a model for human pregnancy (Barry & Anthony, 2008), it can be assumed that even inside the human uterus the amount of light is reduced by more than 95 % when compared to ambient light, and that, therefore, the fetus never experiences light stimuli. This observation has even led to the hypothesis that the very rapid activation of retinal photoreceptors at birth may initiate a sudden brain shift from the prenatal pattern of functions to the neonatal setup (Polese et al., 2022). Nonetheless, a limited number of studies of fetal responsiveness to visual stimulation have been conducted, showing that the switching of a light in front of the maternal abdomen results in induced fetal heart rate accelerations (Smyth, 1965), that fetal movements are present after 26 GA in response to light stimulation (Polishuk et al., 1975), and that the response depends on the initial behavioral state (Kiuchi et al., 2000).

Non ecological investigations also showed that fetuses at 34 GA respond differently to different configurations of laser diodes emitting at 650 nm at high light levels, arranged in a triangular pattern and in contact with maternal tissue (Reid et al., 2017). The triangle was presented with the vertex up or down and moved across the maternal abdomen in a horizontal direction away from the fetal central visual location, for approximately 5 s at an average of 1 cm per second for five times. Results showed that more head turns were made in the direction of the vertex down triangle, and that more head turns were directed toward than away from the vertex down triangle. These findings suggest that almost at term fetuses, even in the absence of visual experience, are able to process visual stimuli and discriminate simple patterns resembling face-like configurations (three blobs arranged like an upside-down triangle) (Reid et al., 2017). This ability, however, is also present in other species having parental care, such as domestic chicks, and monkeys, and in solitary animals with no parental care, such as tortoises, suggesting the presence of an ancient mechanism, ancestral to the evolution of reptiles and mammals, in both solitary and social species (Versace et al., 2020).

Fetal MEG studies investigated the presence of visual evoked brain activity by projecting a flash stimulus (LED array; a sequence of 33 ms duration flash with mean interstimulus interval of 2 s) of 8800 Lux to the maternal abdomen in 10 fetuses at 28 to 36 GA. A response was found in four fetuses respectively at 28, 29, 31, and 36 GA (Eswaran, Wilson, et al., 2002). By using a longer duration stimulus (100 ms or 500 ms, randomly), the same group performed serial visual evoked response (VER) recordings beginning at 28 weeks gestation and recurring every 2 weeks until term (Eswaran et al., 2004). The results of the study showed that fetal P200 (i.e., a positive potential at about 200 ms) is detectable in

most cases as early as 28 weeks and decreases in latency with increased gestation. The authors suggested that the progressive decrease in fP200 latency may reflect the different stages in the physiological development of the visual pathway, given that normally the latencies would shorten with increased myelination (Eswaran et al., 2004).

A functional magnetic resonance imaging (fMRI) (Fulford et al., 2003) study investigated fetal brain activity in response to a visual stimulus in fetuses at term (>36 GA). Scanning was undertaken at this late stage of pregnancy as fetal motion is reduced once the fetal head is engaged within the maternal pelvis. The light stimulus was a red LED cluster of 1100–1200 Lux, and the attenuation through tissue was determined by shining the light through various thicknesses of uncooked chicken breast and recording the resulting light intensity (for a more recent technology to project static and dynamic visual stimuli to the fetus, see (Balasubramanian et al., 2022)). Due to the lack of landmarks in the fetal brain, areas of activation were difficult to determine. However, in four of five cases an area of activation was found within the frontal region with no significant activation detected within the visual areas (Fulford et al., 2003). In fact, the primary visual cortex within the occipital lobe is somewhat undeveloped at birth with the deeper layers showing greater myelination and dendritic branching than the more superficial layers (Huttenlocher, 1990).

2.2. The motor

Three-dimensional ultrasonography (3DUS) was initially introduced in 1989, though still with several limitations, only allowing static observation of the fetal surface. Since 1998, the technique has gained popularity, especially in the field of obstetrics and gynecology, thanks to the digitalization of equipment, which made images more quickly available. More recently, a technique that allowed the three-dimensional image (3D) to be transformed in a real-time mode was introduced and called four-dimensional ultrasonography (4DUS). This technological advance allows the movements of the head, body, and extremities of the fetus to be viewed simultaneously in three dimensions, in real time, from early stages of pregnancy to the last trimester.

The fact that fetuses begin moving very early on was confirmed even with less advanced technology. Spontaneous body movements begin by the end of the second month of gestation, increase in incidence until a plateau is reached around the end of the first trimester, and then gradually decrease until term (Kisilevsky & Low, 1998). The age-related decrease is associated with fewer lower limb movements. The decrease in movement frequency correlates with increased volumetric occupancy of the uterus, such that near term, the fetus occupied approximately 90 % of the intrauterine volume, double that at 20 GA (Hayat et al., 2011).

The study of the spontaneous behaviour of the fetus has always been considered an index of neurological maturation, and the quantitative as well as qualitative aspects of body movements have been analysed and classified into 17 different activities (Kurjak et al., 2008). Most types of movement pattern emerge between 7 and 15 GA (de Vries et al., 1982, 1985). At 7 GA the first observed movement appears consisting of the changing position of the head towards the body (Kurjak et al., 2002). The startle (i.e., a rapid phase contraction of all limb muscles) is the next movement appearing at 8–9 GA (Roodenburg et al., 1991). Shortly afterward, these movements are replaced by general movements of the head, trunk, and extremities, followed by almost simultaneous emergence of isolated limb movements. The presence of the simultaneous onset of arm and leg movements is unexpected because of the long-held principle of a cephalocaudal development in spinal motor functions. After 10 GA, head movements of various types can be seen, and hand to face contact is seen for the first time as an accidental contact. At 11 GA, the opening of the jaw, bending forward of the head, and complex stretch movements appear. During the second trimester of pregnancy, the incidence of body movements increases considerably, however, there are no new movements appearing for the first time (Kurjak et al.,

2008). By term, the number of general movement decreases, and the number of eyelid and mouthing movements increases, including opening/closing of the jaw, swallowing, and chewing (Kurjak et al., 2003).

Starting already at 14 GA, fetuses direct approximately two thirds of their hand movements towards objects in the uterus – their own faces and bodies, the wall of the uterus, and the umbilical cord. Legs extend against uterine wall, arm crosses midline, and the palmar surface extends towards the opposite uterine wall. At 16 GA the frequency of movement decreases. The hand moves around the mouth with frequent sucking, and it moves to specific body parts with following molding of the hand around the body part. There is movement of the hand to the uterine wall, followed by flattening and gliding of the palm against it. There is fingering, grasping, and squeezing the umbilical cord, an activity which probably allows the fetus to begin developing the ability to generate different levels of hand strength. At 20 GA more bilateral movements are present, thus legs extend together against uterine wall, and hands are often held together near the face (Sparling et al., 1999; Sparling & Wilhelm, 1993). Upper and side face touches are declining by age, whereas lower and mouth area touches are increasing (Reissland et al., 2014). At 32 GA, the “hand away from body” movement is observed more often than the other hand movements (Sparling et al., 1999; Sparling & Wilhelm, 1993).

As we have previously seen, to investigate responses to flavors transferred via maternal consumption, Ustun and colleagues (Ustun et al., 2022) took advantage of evidence that complex facial movements begin to develop within the uterus (Reissland et al., 2011; Sato et al., 2014). This facial activity is believed to allow the fetus to gain motor experience necessary for the emergence of several postnatally essential functions like breastfeeding and vocalizing (Finan & Barlow, 1998; Green & Wilson, 2006). At 11 to 12 GA, facial structures, such as nose, orbits, maxilla, and mandible, as well as eyes and mouth, are visible. The most frequent facial movement patterns in the second trimester are isolated eye blinking, grimacing, suckling, and swallowing, whereas mouthing, yawning, tongue expulsion, and smiling could be seen less frequently. During the third trimester, the fetuses began to display decreasing incidence of fetal facial expression (Kurjak et al., 2007). It has been proposed that the facial muscle configurations of fetuses can be linked to the expression of both positive and distressing feelings and may thus be seen as crucial elements for the baby’s early social interactions after birth (Reissland et al., 2011).

2.3. The sensorimotor

The first movements of the fetus give the impression to be randomly distributed across the space around it. The term motor babbling is used to define this random behavior (Caligiore et al., 2008). Interestingly, early in fetal development, quick, progressively larger head flexion movements are repeated, resulting in a “somersault” that enabled the fetus to change position within the uterine cavity (Sparling et al., 1999). These movements may cause unintentional interaction with the body or the uterine environment, eliciting tactile, proprioceptive, and vestibular sensations. Touching causes active stimulation of the part that is actively touching and passive stimulation of the part that is being touched, giving rise to complex reafference phenomena. Broadly speaking, these are activity-dependent sensory effects, the repeated experience of which determines the consolidation of the sensorimotor link (Jékely et al., 2021). Therefore, general movements and isolated movements are essential not only for the development of the motor machinery but also for the development of sensorimotor circuits and sensorimotor mapping (Fagard et al., 2018).

The sensorimotor mapping derives from the associative learning of the contiguity and contingency of movements and of the effects that frequently follow them (i.e., operant behavior) (Brembs, 2009). Thus, when a movement is carried out, all sensory events accompanying it are registered and coded. If a particular movement and a particular sensory event co-occur repeatedly, they are automatically integrated, leading to

a bi-directional association of movements and sensory consequences. Therefore, the activation of one necessarily entails the activation of the other. As suggested by William James (James, 1890), an individual only needs to “think of an intended effect”, and the appropriate action will follow. In the case of the fetuses, it is plausible that the accidental contacts with the body or with the uterine environment start to build sensorimotor associations that, progressively, induce the selection of a repertoire of movements that determine an appreciable amount of sensory consequences. This involves moving from the stage of motor babbling, i.e. random movements, to that of voluntary actions, i.e. to execute movements in order to obtain certain sensory consequences.

The hypothesis that it is the search for sensation, or, in other words, the presence of refference that guides the selection of movements is supported by the fact that the fetus’ movements are increasingly directed toward more sensitive body parts. The mouth and the dermis of the perioral region are the first parts of the body to be innervated starting from 8 GA, and face contacts are seen frequently beginning at 10–12 GA. Very interestingly, Myowa-Yamakoshi and Takeshita (Myowa-Yamakoshi & Takeshita, 2006) observed that once a hand-to-mouth movement was observed, the fetus often repeated the movements 1.5 times, on average, within 30-sec intervals. That is, after moving the arm away from the mouth and taking it below the shoulder level, the arm moved back toward the face within 30 sec. The most frequently observed case was that of one fetus repeating the movements six times in 30 s. Evidence that many babies actually hold and squeeze their umbilical cord inside the womb appears to be further indication of this sensation-seeking. In fact, the modulation of the blood flow, a consequence of the constriction of the umbilical cord, probably generates sensations unknown to those who live outside the maternal uterus, which may be interesting for the fetus, and, therefore, desired. These observations suggest that the mechanism that guides movement selection depends on the presence of contiguity and contingency between movement and sensory effects in order to establish sensorimotor associations. The refference principle claims that, once this link is established, sensory effects can be predicted and used to plan action (Jékely et al., 2021). Indeed, the establishment of a sensorial-driven functionality is supported by the finding that as the fetuses mature from second to third trimester of pregnancy, they develop from a sequence of mouth opening following touch, to mouth opening occurring before touch, suggesting a development from reaction to anticipation (Reissland et al., 2014) (see paragraph “Space coding” for the discussion on the role of the amniotic fluid wave induced by the approaching hand in anticipating the instant of touch). The best example of action planning anticipating the related sensory consequences is given by an amazing kinematic study of hand movements towards the mouth and the eyes in fetuses at 14, 18 and 22 GA (Zoia et al., 2007). It is known that at 16–18 weeks, the fetus starts touching its eyelids. Given the presence of rods and future cones by the end of the 12 GA, it is probable that rubbing the eyelids may generate flashes of light in the fetus (Fagard et al., 2018). Thus, mouth and eyes are the most frequent targets of hand movements during the second trimester of pregnancy. The results of the kinematic study showed that by 18 GA, movement duration and time to peak velocity of movements directed towards the mouth and eyes are comparable. In contrast, by 22 GA, peak velocity for movements to the eyes is earlier and lower than that to the mouth, indicating that acceleration and deceleration phases seem to be planned according to the size and/or delicacy of the target. These findings suggest that during the stage of motor babbling preceding the 22 GA, the fetus collected information about the sensory consequences of reaching the eye at different velocities and used these different sensations to adjust the approach of the hand to the smaller and more delicate target. The observed differences in kinematics may suggest a primitive predictive process already operating in the fetus, in which the sensory consequences of a movement are anticipated and used to plan an action related to the nature of the target (Zoia et al., 2007). That is, at the end of the second trimester of pregnancy, the movement goal is selected before the movement starts, and

the movement parameters are adjusted to the characteristics of the goal.

Altogether, these data indicate that intrauterine behavior develops to provide the activity-dependent input to the sensory system. This makes it possible for the fetus to select movements and build a repertoire of preferred actions capable of providing the desired sensations.

3. After birth and within the first year of life

At birth, the newborn is abruptly exposed to the external world. Stimuli are no longer buffered by the pregnancy tissues and fluids, and the extrauterine environment directly affects the newborn’ senses with all possible forms of physical energy: Sound waves, electromagnetic radiations, mechanical, thermal, chemical stimuli, and full force of gravity. Furthermore, most events and objects provide the senses with a complex combination of visual, auditory, tactile, and olfactory stimulation, which required the brain to evolve to extract the unified world experienced by the adult. There are conflicting hypotheses regarding the process that leads to the development of this ability. For much of the twentieth century, most developmental scientists believed that newborns had to gradually learn how to integrate and coordinate information from their various sensory systems, which were completely separate at birth. The infant was thought to achieve this integration by interacting with objects, experiencing simultaneous feedback from several senses, and associating, assimilating, or calibrating one sense with another (Birch & Lefford, 1963; Freides, 1974; Piaget, 1952) (see also (Streri & de Hevia, 2023)). On the other hand, since the eighteenth century, philosophers have proposed that the newborn does not differentiate stimuli from different modalities, and that the total amount of energy, summoned across all modalities, exists in the common “sensorium” (Rousseau, 1762). William James (James, 1890) has provided a colorful description of the possible sensory experience at birth “... the undeniable fact being that any number of impressions, from any number of sensory sources, falling simultaneously on a mind which has not yet experienced them separately, will fuse into a single undivided object for that mind ... The baby, assailed by eyes, ears, nose, skin, and entrails at once, feels it all as one great blooming, buzzing confusion”. In the last thirty years scientists working in the field of developmental psychology described this initial confusion as “synesthesia” (Maurer, 1993), literally a “union of the senses”, a condition found in adults wherein stimulation of one sense evokes an additional arbitrary stimulation of another sense (Simner, 2012; Ward, 2013). The neonatal-synesthesia hypothesis suggests that synesthesia may occur at high rates during infancy because of increased functional connectivity in the infant brain relative to the adult brain (Neville, 1995), and then dissipates as the result of experience-dependent synaptic pruning and/or inhibition of cross-sensory neural connections (Maurer et al., 2013). According to this idea, the newborn is aware of changes in the pattern of energy and recognizes some patterns that were experienced before but is unaware of which modality produced that pattern. This allows newborns to detect cross-modal correspondences when stimuli from different modalities produce common patterns of energy change. Thus, when the baby is habituated to an auditory stimulus, he or she simultaneously perceives and is habituated to the corresponding visual stimulus. As an example, Lewkowicz and Turkewitz (Lewkowicz & Turkewitz, 1980) showed that 3-wk-old infants ignore differences between lights and sounds and instead respond to auditory and visual stimuli as more or less similar depending on their intensity. Evidence indicated that the link between auditory and visual information extends to synchrony, showing that, by 4 weeks, infants show sensitivity to synchrony between visible and audible impacts (Bahrick, 2001). Further evidence that sensory modalities do not need to be associated by experience and learning in order to be coordinated, is provided by results showing that two-day-old newborns can visually recognize the shape of an object that they have previously manipulated with their hand, out of sight (Streri & Gentaz, 2004), and that they prefer to look at body-related, synchronous visual-tactile stimuli (Filippetti et al., 2013).

Longitudinal studies indicated that the development of cross-modal perception is U-shaped. Near birth, newborns showed effective cross-modal information linking, then failed at similar tasks later in infancy, and then appeared to gradually acquire cross-modal links in the second half of the first year of life (Maurer & Mondloch, 2005). This is evident in studies that used the same procedure at different ages and found success earlier in infancy followed by failure later in infancy (Pickens et al., 1994; Streri & Pêcheux, 1986). The interpretation of the phenomenon is that the decrement in cross-modal perception diminishes as transient connections are pruned (Chechik et al., 1999) and as more specialized cortex exerts more control (Vasung et al., 2019). This process determines the separation of various sensory modalities, resulting in faster and more efficient information processing, and is thus extremely adaptive (Baron-Cohen, 1996; Karmiloff-Smith, 1994). Thereafter, the major task of perceptual development then becomes to interrelate/differentiate senses on the base of experience-dependent information (Lickliter, 2011).

Perhaps the most affected sense by the transition to the extrauterine environment is vision, which calls for a more thorough description as detailed in the paragraph that follows.

3.0.1. Vision

At birth, electromagnetic radiation strikes the eyes directly, with no barriers in between. The peripheral retina of the eye is reasonably well developed, but the central retina (the macular region and the fovea), which allows for fine detail detection, is immature (Abramov et al., 1982). The period of retinal maturation extends beyond full term birth to the first few postnatal months and then proceeds more gradually into early childhood (for a fascinating and clear description of the development of connections in the mammalian visual system, see Shatz, 1992). The retina of a neonate born at term is approximately half the volume of the adult retina and shows significant immaturities in both structure and function (Hendrickson & Drucker, 1992). Thus, the visual information detected by the newborn is 10–30 times poorer than that in the adult, as acuity, scanning abilities, contrast sensitivity, and color discrimination, are limited at birth. Consequently, the newborn may leave a stationary object unnoticed for acuity reasons. A moving object does not run the same risk, since its motion adds potentially to the information separating it from the background. Neonates' field of view is also smaller, meaning that they appear not to attend to visual information too far distant or too far in the periphery, and they lack stereopsis, the perception of depth in near space from binocular disparity (Johnson, 2011). However, thanks to the presence of parental care, their poor vision is adequate to perceive the world of interest to them. They do not need to see things clearly at a distance, since the most important visual stimuli are to be found in close proximity. The visual preference method was used to examine the kinds of visual discrimination versus neonates can perform and the kinds of spontaneous preferences they show. It consists in presenting newborns with pairs of patterns and recording the proportion of fixation times per exposure. The preference for a novel stimulus is commonly interpreted to indicate the infant's recognition of the familiar stimulus and, thus, the ability to discriminate (Fantz, 1964). In newborns of a few hours of life, among others, preferences are for patterned versus un-patterned stimuli, curvature versus rectilinear patterns, moving versus static patterns, three-dimensional versus two-dimensional forms, and high- versus low-contrast patterns (Johnson, 2011). In addition, some organizational features of visual perception are present at birth, as infants show knowledge of the constancy of the size and shape of objects (Slater, 2002). Finally, newborns prefer to look at faces and face-like forms relative to other visual stimuli (Turati et al., 2002; Valenza et al., 1996), a preference already present during prenatal life (Reid et al., 2017) and common to social and non-social species (Versace et al., 2020).

Several are the electrophysiological techniques that may be used to measure brain activity in newborns and infants. Among them, fMRI is challenging on a practical level due to the loud noises associated with

MRI as well as the need for the infant to remain motionless during the scan. As a result, newborn fMRI studies are usually conducted during natural sleep, which limits their ability to directly analyze brain activities during visual tasks. In contrast, MEG, a previously described method also used for fetal research, offers a more appropriate environment for studying brain activities in awake newborns because it is quiet and less restrictive. It was mainly used to study auditory and somatosensory stimulation, and very few studies used MEG to study primary visual evoked fields (VEFs) or evoked responses to visual stimuli in young children (Chen et al., 2019). Specifically, two studies have examined habituation of visual response in newborns using a train of light flashes, showing decreased neonatal VEFs (i.e., an index of habituation) to successive light flashes (Matuz et al., 2012; Sheridan et al., 2008). An electrophysiological technique that can be used in the newborn but was not possible in the fetus is the recording of event-related potentials (ERPs). ERPs are voltage oscillations in scalp-recorded electroencephalographic (EEG) data that are time-locked with an event of interest. Stimuli are presented briefly and repeatedly to each participant, and then all trials for a particular group or stimulus type are averaged together to identify the ERP. ERP studies of recognition memory used an oddball procedure in which two unfamiliar visual stimuli were presented briefly and with unequal frequency. The consistent finding was a larger Nc component to the infrequently presented "oddball" stimulus than to the frequently presented "standard" stimulus (Karrer & Monti, 1995). The Nc is a component of negative polarity located over frontal and central electrodes with a peak latency of between 400 and 800 ms following stimulus onset. Subsequently, the use of high-density electroencephalogram recording, and cortical source localization techniques identified areas of prefrontal cortex including the anterior cingulate as likely sources of the Nc component (Reynolds & Richards, 2009). By simultaneously measuring visual preference behavior and ERPs, Reynolds and colleagues (Reynolds et al., 2010) showed that infants who demonstrated novelty preferences in paired comparison trials demonstrated greater amplitude Nc components across tasks than infants who did not demonstrate novelty preferences.

In the next paragraphs it will be described how the sensorimotor knowledge accumulated through interaction with the intrauterine environment may integrate at birth with vision, the new sense available, to act and perceive in the new environment.

3.1. Reaching

There are no movements observed in neonatal life that are not present in fetal life. The most frequent are scowling, eye and mouth opening, and hand to face, hand to eye and hand to head movements. Also present are blinking, yawning, and tongue expulsion (Kurjak et al., 2004). The developmental trend in self-touching includes a tendency to go from rostral to caudal targets, from dorsal to palmar hand contacts, and from touch to grasp behaviors (Thomas et al., 2014). Sucking is an important skill that is already present during intrauterine life and that newborns master by skillfully regulating the sucking pressure (Craig & Lee, 1999).

At birth, however, the newborn's environmental constraints shift dramatically, transitioning from an aquatic to an aerial medium. Because the newborn has many new parameters to integrate into its movements, this could explain the apparent regression in limbs motor control (Fagard et al., 2018). Evidence of the reorganization phase necessary to re-adapt arm movement to the novel environment is provided by the finding that the longer movement duration and deceleration time found at 22 weeks of gestation for movements towards the eye rather than the mouth (Zoia et al., 2007), re-emerge only at four months of postnatal life (Zoia et al., 2013). During this reorganization phase, the newborn must explore selective strategies for movement, discovering useful patterns of reaching which account for sensorimotor interactions. Indeed, in the new environment, vision is a new source of information for perceiving arm posture. This information must be integrated with that provided by proprioception, which guided movements during

prenatal life, a learning process that may require a few months. As a result, although successful reaching does not appear until around 4 months of life, findings indicated that since birth a higher proportion of movements performed while the infant fixated an object was forward extended than otherwise and aimed closer to the object (von Hofsten, 1982). It has been proposed that when the hand moves toward the object of interest it enters into the visual field and its movements can therefore be perceived visually. As a consequence, this behavior makes it possible for the newborn infant to begin exploring the relationship between proprioception and the newly acquired vision (von Hofsten, 2009). An example of a very early ability to control arm movements on the basis of visual information was provided by Van der Meer (Van Der Meer, 1997). In the experiment, twenty-day old newborns laid supine, and their spontaneous arm-waving movements were measured in the dark. A fronto-parallel, horizontal beam of light was passed in front of the baby in such a way that the light was not visible unless the child happened to put their hand into the beam. It was discovered that after the first event of this type, the children repeatedly placed their hand into the beam, and when the beam moved, they moved their hand improving their chances of having it illuminated.

Just as the fetus becomes able to reach the eye without hurting itself, so the newborn becomes able to move its arm to see something in a dark room, probably not yet knowing it is its arm. All of these are examples of actions executed to provide the activity-dependent input to the sensory system. They are examples of goal-directed, voluntary actions, emerged from the coding of the contingency between a motor command and the perception of its sensory consequences. Furthermore, since it has been claimed that the link between the motor and sensory systems is bidirectional, the sensory stimulus must be classified according to motor knowledge. These assumptions served as the basis for research on 2-day-old newborns (Craighero et al., 2020) which considered evidence that fetuses move with the typical velocity profile of biological motion (Zoja et al., 2007). Biological motion is characterized by a fast-velocity initial phase and a low-velocity final phase (Jeannerod, 1984). The study showed that 2-day-old newborns can discriminate dots configurations (Point-Light Displays, PLD) of the same shape, moving along the same trajectory with the same movement duration, based on their different motion, i.e. biological (i.e., accelerated-decelerated) versus non-biological (i.e., constant velocity). This ability, however, emerges only after the repeated visual presentation of the different kinematics, and manifests itself as a preference for the biological motion, implying a fast plasticity of the sensorimotor system in linking an already acquired motor knowledge (in the intrauterine environment) with a newly experienced congruent visual stimulation (in the external environment) (Craighero et al., 2020). These results require a reformulation of the direct matching hypothesis (Iacoboni et al., 1999; Rizzolatti et al., 2001; Rizzolatti & Craighero, 2004) by suggesting that the relationship between perception and action does not require only action development (Libertus & Needham, 2010) but also the accumulation of sufficient perceptual experience. This may be especially true if the association is based on subtle kinematic features visually perceived (Craighero et al., 2020). Direct evidence of the involvement of the sensorimotor system during observation of PLD stimuli moving with biological motion early in development was provided by an EEG study showing an attenuation of sensorimotor alpha band activity in 9-month-old infants (Quadrelli et al., 2019).

3.2. Grasping

Already during the first month of life, the presence of an object appears to be a crucial clue to suggest the presence of a voluntary action and activate the sensorimotor system. This is confirmed by the evidence that the mere presence of a to-be-grasped object induce attenuation of the sensorimotor alpha band activity in 9-month-old infants (Quadrelli et al., 2019; Southgate et al., 2009). The existence of a sensorimotor identity between an object with certain intrinsic properties and the appropriate action for grasping that object is attested by

neurophysiological findings in the monkey showing the presence of sensorimotor neurons. In ventral premotor area F5 there are motor neurons discharging in association with goal-directed actions such as grasping, manipulating, tearing, and holding. In addition to their motor discharge, several F5 neurons are also activated when the monkey observes graspable objects whose intrinsic properties are congruent with the type of movement (e.g., small objects/precision grip, big objects/whole hand prehension) (Murata et al., 1997). Numerous neuroimaging (Chao & Martin, 2000; Grafton et al., 1997; Grèzes & Decety, 2002; Martin et al., 1996), neurophysiological (Franca et al., 2012; Makris et al., 2011), and behavioral (Craighero et al., 1996, 1998, 1999; Ellis & Tucker, 2000; Symes et al., 2007; Tucker & Ellis, 1998) studies demonstrated that this representational sharing is present also in adult humans, indicating that observing a graspable object or grasping that object are encoded in the same way.

Although the newborn is not yet able to reach and grasp objects in the extrauterine environment, this sensorimotor knowledge is formed during intrauterine life and seems to be transferred to the categorization of visual stimuli, as shown by a preferential looking experiment in 2-day-old newborns (Craighero et al., 2011). Results indicated that they orient more frequently and spend more time looking a video of a moving hand that opens compared to a video of a moving hand that remains closed, but only when the movement is directed away from the body and toward the external world. In addition, newborns prefer the away from the body stimulus only when an object is present at the end of the movement, thus preferring a hand movement that may develop into a purposeful one (Craighero et al., 2011). The link between the execution of an action and the observation of a hand performing that action is also demonstrated by the presence of sensorimotor neurons in the monkey. A subset of motor neurons in premotor area F5 is active when the monkey acts on an object and when it observes another monkey or the experimenter performing a similar goal-directed action (di Pellegrino et al., 1992). Some of them discharge when the animal also hears the sound related to the action, thus encoding the actions regardless of whether they are performed, heard, or seen, and regardless of the identity of the agent (Keyesers et al., 2003; Kohler et al., 2002). The multisensory link with the execution of the action is also evident in the newborn from the results of an electrophysiological study (Paulus et al., 2012). Eight-month-old infants were trained to use a novel rattle that produced a specific sound when shaken, and familiarized with another, not action-related sound. After this training phase, infants displayed stronger attenuation of sensorimotor alpha band activity when listening to the action-related sound than when hearing the other sound, indicating that the perception of the sensory consequences of a known action activates the motor system.

Over the last twenty years, an impressive number of articles have also demonstrated in adult humans the presence of a sensorimotor identity between action execution and action perception (see some of the most recent reviews and meta-analysis, (Hardwick et al., 2018; Hari, 2006; Keyesers et al., 2018; Naish et al., 2014; Vanderwert et al., 2013), strongly suggesting that on a neuronal and behavioral level, grasping an object or perceiving someone grasping that object are encoded in the same way.

3.3. Orienting of attention

The newborn gains awareness during prenatal life that the sensory consequences are primarily present at the point where the movement stops, which corresponds to the position at which the target is touched. The results of preferential looking technique experiments in 2-day-old newborns (Craighero, Lunghi, et al., 2016) indicated that this knowledge is automatically transferred to visual perception, consequently labelling the end of the translational displacement as the most salient position in the visual space. Specifically, infants were able to discriminate two translating meaningless PLD videos in which the shape of one of them changes compared to that of the other along the trajectory, but only when stimuli differed at the end of the movement. These data

suggest that movement translational components induce newborns to allocate attention at the end of the observed movement. The evidence of this attentional bias (Craighero et al., 2011; Craighero, Lunghi, et al., 2016) suggested that this primitive form of sensorimotor link may be the origin of the proactive gaze (Craighero et al., 2020). This term refers to the ability to shift gaze from a reaching hand to the goal of the action before the hand arrives at its goal, exactly as it happens when individuals perform the task themselves (Flanagan & Johansson, 2003; Rotman et al., 2006). The possibility of viewing a shift in attention to the end of a movement trajectory as a precursor of predictive gaze comes from findings indicating that the mechanisms underpinning oculomotor programming and those responsible for spatial attention share similar structures (Corbetta, 1998; Hoffman & Subramaniam, 1995; Kowler et al., 1995; Kustov & Robinson, 1996; Nobre et al., 2000; Rizzolatti, 1983), and that a peripheral oculomotor impairment (Craighero et al., 2001) or a forced posture of the eye (Craighero et al., 2004), cause the inability to shift attention. These findings support the premotor theory of attention, which holds that visuospatial attention and eye movement programming are encoded in the same way (Craighero & Rizzolatti, 2005; Rizzolatti et al., 1987; Rizzolatti & Craighero, 1998).

It is thus possible that the attentional unbalance observed in newborns, attributed to knowledge of the region of space richer in sensory information, may develop into the ability to shift the fovea to the goal ahead of the hand during reaching movements, in order to seek out online information required to correctly perform the movement (Craighero, Lunghi, et al., 2016). As hypothesized so far, however, this possibility must depend on the ability to effectively perform a reaching movement. Only the consolidation of sensorimotor representation in the extrauterine space enriched by vision can lead to the development of proactive gaze, either during execution or during observation. Evidence that the development of fine motor skills is essential for the development of gaze/attention orientation is provided by a study by Falck-Ytter and colleagues (Falck-Ytter et al., 2006). They showed that, during video presentations of an actor's hand moving toys into a bucket, adults as well as 12-month-olds shifted gaze proactively to the goal of the action. The 6-month-old infants, however, did not do that, as they do not yet systematically move objects from a position to another (Berthier & Keen, 2006; Corbetta & Snapp-Childs, 2009; Gonçalves et al., 2013), confirming that the development of the two abilities is strictly related.

Further studies considered gaze latency as an indication of orienting of attention in infants, in the presence of static stimuli simply suggesting a direction, such as the direction of gaze (Farroni et al., 2004), a walking direction (Lunghi et al., 2019), or the abrupt appearance of a cue in the periphery (Xie & Richards, 2017). These studies showed faster saccade latencies, and larger P1 ERP component in response to targets appearing at suggested spatial locations. Therefore, newborns from birth demonstrate greater efficiency in moving their eyes towards the most interesting position, accompanied by an enhancement of neural activity related to visual processing of stimuli appearing in that position. These findings agree with the prediction of the premotor theory of attention claiming that oculomotor programming makes the individual ready to respond and facilitates the processing of incoming stimuli spatially congruent with the motor program (Craighero & Rizzolatti, 2005). At a neurophysiological level, evidence of this sensorimotor identity is provided by the presence of visual and visuomotor neurons in the monkey frontal eye field (FEF), an oculomotor area within prefrontal cortex. Beside the presence of neurons firing in association with eye movements (motor neurons), in the same region there are also neurons responding to visual stimuli (visual neurons), and neurons with both visual- and movement-related activity (visuomotor neurons) (Bruce, 1988; Bruce & Goldberg, 1985; Goldberg & Segraves, 1989). The latter are activated in exactly the same way every time the monkey moves its eyes towards a specific region of the visual space, and when a stimulus appears in that region. Seeing something in one spatial position or moving your eyes to that position are encoded in the same way.

3.4. Space coding

Most languages distinguish between words that refer to something a short distance away and terms that refer to something a long distance away. In English, far is who or what is at a great distance, and near is who or what is close to where one is. In the neuroscientific literature the terms used are, respectively, extrapersonal space and peripersonal space. The evidence from neuropsychological (Berti & Frassinetti, 2000; Cowey et al., 1994; Halligan & Marshall, 1991; Pegna et al., 2001), behavioral (Craighero & Marini, 2021; Farnè & Ladavas, 2000; Gamberini et al., 2008, 2013; Longo & Lourenco, 2006), and neurophysiological (Maravita et al., 2001, 2002) studies suggests that the binary distinction of space is based on functional parameters rather than metrical ones. That is, peripersonal space is the space in which it is possible to reach objects and act on them, with the hand, with a stick, or with a remote control. Instead, extrapersonal space is the space that you can only perceive (Craighero, 2014). Moreover, the events present in the peripersonal space are predictive of potential pleasant or dangerous interactions to which it is necessary to pay attention in order to respond adequately. For example, if an insect comes dangerously close to my face, I have to quickly move my head to the opposite side. Also for this example there is evidence of a sensorimotor identity at a neurophysiological level. In the monkey ventral premotor area F4, most neurons discharge in association with movements of the head or the arm. A large proportion of them also respond to all possible sensory stimuli (tactile, visual, acoustic) present on the skin or close to the skin, in correspondence of a specific tactile receptive field (Fogassi et al., 1996; Graziano et al., 1997, 1999; Rizzolatti et al., 1988). Thus, the discharge of these neurons reflects a potential action directed toward (or away from) a region of peripersonal space, as well as the presence of any potential stimulus existing in that region. Perceiving a stimulus in that area or moving toward or away from that area are thus encoded in the same way.

The fetus in the uterus experiences only the peripersonal space, as every stimulus is conveyed by the amniotic fluid that surrounds it. Any movement of the fetus turns into a displacement of the amniotic fluid that can be perceived by other body parts. When the hand goes towards the wall of the uterus, the water resistance changes progressively as the hand approaches it, anticipating the instant of touch. The same occurs when the hand moves towards a body part. Furthermore, because of the movement of the liquid, the portion that will be touched also has information about the touch in advance. As previously mentioned, the amniotic fluid also carries sounds, which are translated into vibrations of the liquid and perceived first as tactile stimulations and then as sounds, through bone conduction. In this way, the fetus experiences movement, touch, and sound through the same medium, which provides an increasing level of stimulation intensity as the event approaches the body, allowing to predict the instant of contact. It is plausible, therefore, that even before birth, the intensity of the stimulus is translated into information about the distance from the body. Moreover, based on what has been said about synesthesia in newborns, visual information, which is new to the infant, should take advantage of this knowledge and be readily coded as approaching based on optical flow, an event easily assimilated to the amniotic fluid wave induced by an approaching hand. Evidence of this possibility is the presence of directionally appropriate head movements under rough optical flow in 3-day-old newborns, considered an index of a primitive postural reaction to an approaching visual stimulus (Jouen, 1988; Jouen & Lepecq, 1989), and the presence from birth of a rudimentary coupling between optical flow and stepping (Barbu-Roth et al., 2009).

Thus, if already before birth the peripersonal space is codified in a multisensory way, and intensity variation is considered a cue of the stimulus' distance, then this knowledge must manifest itself soon after birth. A series of studies confirmed this prediction in 2-day-old newborns (Orioli et al., 2019; Ronga et al., 2021). They applied an adapted version of the audio-tactile interaction task developed by Canzoneri and colleagues (Canzoneri et al., 2012). In the original task, the adult

participants were presented with a sound of raising intensity. During the presentation of the auditory stimulus, they felt a touch on their hand, occurring when the sound source was perceived at different distances from the hand. The participants were asked to verbally respond to the touch as rapidly as possible. The responses were faster when the sound was perceived within a limited distance from the hand, i.e. within the peripersonal space. As with the proactive gaze, it is the perception of the movement that leads to directing attention towards the final phase of the movement, facilitating the response to any stimulus spatially congruent with the end of movement trajectory (Craighero & Mele, 2021). These findings imply that attention is automatically directed toward the end of the movement of a dynamic acoustic stimulus as well as of a dynamic visual stimulus. In infant experiments, individual sounds at different intensities were presented, rather than a single sound whose intensity varied to mimic sound source movement. Similarly to adults, infants showed faster reaction times to a touch when the touch was presented with a sound louder than a certain critical intensity (Orioli et al., 2019). The authors speculated that this critical sound intensity could be considered as the boundary of a rudimentary multisensory representation of peripersonal space in newborns. A further study (Ronga et al., 2021) recorded event-related potentials (ERPs) in 2-day-old newborns and in adults while participants were receiving tactile stimuli on the hand dorsum, and hearing auditory stimuli presented either near (<5 cm) or far (140 cm) from the stimulated hand. Very similar results were found in both groups. Specifically, results showed superadditive responses to bimodal stimuli (ERPs exceeding the sum of unimodal responses (Bernasconi et al., 2018; Noel et al., 2019)) greater when the auditory stimuli were presented close to the body. Thus, it appears that the perception of peripersonal space requires more than the presence of a static unimodal stimulus. An isolated and unexpected tactile stimulus or sound can be viewed as an isolated sensory experience caused by an unknown source, lacking spatial characteristics. Conversely, the simultaneous presence of a tactile stimulus and a sound near the body may provide the illusion of being in the presence of a three-dimensional object, to which multisensory experiences are attributed. In Orioli et al. (Orioli et al., 2019), the auditory stimulus was presented before the tactile one. In Ronga et al. (Ronga et al., 2021) the auditory stimuli were delivered 40 ms after the tactile stimuli to compensate the delayed latency in reaching the primary sensory cortex of tactile stimulation. Such a delay is further increased in newborns, due to the incomplete myelination of the pathways and to the immature synaptic functioning. However, there is no certainty that this 40 ms correction was sufficient to prevent the unconscious perception of a temporal asynchrony between the stimulations, namely acoustic first, then tactile. As a consequence, it is plausible that in both studies the temporal asynchrony produced the illusion of a moving stimulus approaching and then touching the body. In Ronga et al. (Ronga et al., 2021), the very short temporal asynchrony allowed the illusion of movement only when the acoustic stimulus was perceived so close as to be compatible with the duration of the spatial displacement required to touch the body. The same in Orioli et al. (Orioli et al., 2019), the responses were present only when the sound was louder than a certain critical intensity, i.e. perceived very close. Supporting the possibility that the effect was due to the illusion of a moving stimulus, are the results of an audio-tactile psychophysical task in adults suggesting that the duration of the spatial displacement required to touch the body depends on the velocity of the approaching stimulus. Accordingly, the findings showed that the responses were present at a boundary distance of 52 cm when the acoustic stimulus moved at 25 cm/s, and at a boundary distance of 77 cm when the velocity reached 75 cm/s (Noel et al., 2018).

4. Conclusion

The aim of this review is to integrate information from different and apparently distant disciplines to functionally describe the interaction of the fetus and newborn with surrounding objects. The functional

description is necessary when dealing with developing organisms, as the presence of anatomically and physiologically primitive structures does not guarantee that they are already functional. Therefore, effective interaction with objects can be demonstrated exclusively by the presence of a physiological or behavioral modification related to the stimulus. This type of evidence is extremely difficult to obtain in the study of fetuses and therefore knowledge of experiences during intrauterine life is rather limited.

Despite these limitations, the first part of the review seeks to provide as precise a description as possible of i) the sensory environment and the functional development of sensory skills, ii) the functional development of motor skills, and iii) how activity-dependent sensory effects may give rise to the sensorimotor binding. It is proposed that the associative learning between the execution of a movement and its sensory consequences may induce the selection of a repertoire of movements that determine an appreciable amount of sensory consequences. This involves moving from the stage of motor babbling, i.e., random movements, to that of voluntary actions, i.e., to execute movements to obtain expected sensory consequences. Experimental evidence indicates that this ability is already present in 22-week fetuses.

Although in common sense birth is considered the beginning of the possibility of perceiving and acting in the world, it is located along a continuum in which previous experiences have a fundamental role in the interaction with objects in the extrauterine environment. This knowledge, however, must be updated with the transition from the aquatic to the aerial environment, and with the presence of a new type of stimulation, light, which is practically absent in the uterus. The second part of this review attempts to describe this passage and suggests the role that the established sensorimotor link has in the origin of some fundamental cognitive functions for interaction with the world, such as the ability to locate objects in space or to direct attention towards the spatial position richest in information.

By concluding, this narrative review used an embodied approach to describe the development of sensorimotor and perceptual abilities in humans during prenatal and perinatal life. The embodied approach argues that interaction with the environment plays a crucial role in behavior and brain development, and that the presence of sensory effects generated by movements is fundamental in this process. Thus, the overarching objective of this review is to provide enough insight into how behavior develops to offer suggestions for future neuroscientific research capable of shedding light on the transition from the transitory fetal circuit, rich in subplate neurons, to the immature but progressively developing permanent cortical circuit.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

References

- Abramov, I., Gordon, J., Hendrickson, A., Hainline, L., Dobson, V., & Labossiere, E. (1982). The retina of the newborn human infant. *Science*, 217(4556). <https://doi.org/10.1126/science.6178160>
- Adler, J. (1965). Chemotaxis in *Escherichia coli*. *Cold Spring Harbor Symposia on Quantitative Biology*, 30. <https://doi.org/10.1101/SQB.1965.030.01.030>
- Alabduljalil, T., Westall, C. A., Reginald, A., Farsi, S., Chiu, S. J., Arshavsky, A., Toth, C. A., & Lam, W. C. (2019). Demonstration of anatomical development of the human macula within the first 5 years of life using handheld OCT. *International Ophthalmology*, 39(7). <https://doi.org/10.1007/s10792-018-0966-3>
- Arroyo, D. A., & Feller, M. B. (2016). Spatiotemporal features of retinal waves instruct the wiring of the visual circuitry. *Frontiers in Neural Circuits*. (Vol. 10)(JUL2016). <https://doi.org/10.3389/fncir.2016.00054>
- Bahrick, L. E. (2001). Increasing specificity in perceptual development: infants' detection of nested levels of multimodal stimulation. *Journal of Experimental Child Psychology*, 79(3), 253–270. <https://doi.org/10.1006/jecp.2000.2588>
- Balasubramanian, K. K., Diotalevi, F., Lorini, C., Cavallo, A., Pretti, N., Paladini, D., Torazza, D., Becchio, C., & Crepaldi, M. (2022). A transcutaneous fetal visual stimulator. *IEEE Access*, 10. <https://doi.org/10.1109/ACCESS.2022.3169778>
- Barbu-Roth, M., Anderson, D. I., Després, A., Provasi, J., Cabrol, D., & Campos, J. J. (2009). Neonatal stepping in relation to terrestrial optic flow. *Child Development*, 80(1), 8–14. <https://doi.org/10.1111/j.1467-8624.2008.01241.x>
- Baron-Cohen, S. (1996). Is there a normal phase of synaesthesia in development. *Psyche*, 2(27).
- Barry, J. S., & Anthony, R. V. (2008). The pregnant sheep as a model for human pregnancy. *Theriogenology*, 69(1). <https://doi.org/10.1016/j.theriogenology.2007.09.021>
- Belliemi, C. V., Bagnoli, F., Perrone, S., Caparelli, N., Cordelli, D. M., Melissa, B., & Buonocore, G. (2003). Long-term effects of antepartum bed rest on offspring. *Biology of the Neonate*, 84(2). <https://doi.org/10.1159/000071949>
- Bernasconi, F., Noel, J. P., Park, H. D., Faivre, N., Seeck, M., Spinelli, L., Schaller, K., Blanke, O., & Serino, A. (2018). Audio-tactile and peripersonal space processing around the trunk in human parietal and temporal cortex: An intracranial EEG study. *Cerebral Cortex*, 28(9). <https://doi.org/10.1093/cercor/bhy156>
- Berthier, N. E., & Keen, R. (2006). Development of reaching in infancy. *Experimental Brain Research*, 169(4), 507–518. <https://doi.org/10.1007/s00221-005-0169-9>
- Berti, A., & Frassinetti, F. (2000). When far becomes near: Remapping of space by tool use. *Journal of Cognitive Neuroscience*, 12(3). <https://doi.org/10.1162/089982900562237>
- Birch, H. G., & Lefford, A. (1963). Intersensory development in children. *Monographs of the Society for Research in Child Development*, 28(5). <https://doi.org/10.2307/1165681>
- Birnholtz, J. C., & Benacerraf, B. R. (1983). The development of human fetal hearing. *Science*, 222(4623), 516–518. <https://doi.org/10.1126/science.6623091>
- Brembs, B. (2009). The importance of being active. *Journal of Neurogenetics*, 23(1–2). <https://doi.org/10.1080/01677060802471643>
- Bruce, C. J. (1988). Single neuron activity in the monkey's prefrontal cortex. In P. Rakic, & W. Singer (Eds.), *Neurobiology of neocortex* (pp. 297–329). John Wiley & Sons Limited.
- Bruce, C. J., & Goldberg, M. E. (1985). Primate frontal eye fields. I. Single neurons discharging before saccades. *Journal of Neurophysiology*, 53(3), 603–635. <https://doi.org/10.1152/jn.1985.53.3.603>
- Caligiore, D., Ferrauto, T., Parisi, D., Accornero, N., Capozza, M., & Baldassarre, G. (2008). Using motor babbling and hebb rules for modeling the development of reaching with obstacles and grasping. *International Conference on Cognitive Systems*.
- Canzonieri, E., Magosso, E., & Serino, A. (2012). Dynamic sounds capture the boundaries of peripersonal space representation in humans. *PLoS One*, 7(9). <https://doi.org/10.1371/journal.pone.0044306>
- Carlsen, R., & Lickliter, R. (1999). Augmented prenatal tactile and vestibular stimulation alters postnatal auditory and visual responsiveness in bobwhite quail chicks. *Developmental Psychobiology*, 35(3). [https://doi.org/10.1002/\(SICI\)1098-2302\(199911\)35:3<215::AID-DEV6>3.0.CO;2-O](https://doi.org/10.1002/(SICI)1098-2302(199911)35:3<215::AID-DEV6>3.0.CO;2-O)
- Chao, L. L., & Martin, A. (2000). Representation of manipulable man-made objects in the dorsal stream. *NeuroImage*, 12(4), 478–484. <https://doi.org/10.1006/nimg.2000.0635>
- Chechik, G., Meilijson, I., & Ruppín, E. (1999). Neuronal regulation: A mechanism for synaptic pruning during brain maturation. *Neural Computation*, 11(8), 2061–2080. <https://doi.org/10.1162/089976699300016089>
- Chen, Y. H., Saby, J., Kuschner, E., Gaetz, W., Edgar, J. C., & Roberts, T. P. L. (2019). Magnetoencephalography and the infant brain. In *NeuroImage*. <https://doi.org/10.1016/j.neuroimage.2019.01.059>
- Corbetta, D., & Snapp-Childs, W. (2009). Seeing and touching: The role of sensory-motor experience on the development of infant reaching. *Infant Behavior and Development*, 32(1), 44–58. <https://doi.org/10.1016/j.infbeh.2008.10.004>
- Corbetta, M. (1998). Frontoparietal cortical networks for directing attention and the eye to visual locations: Identical, independent, or overlapping neural systems? *Proceedings of the National Academy of Sciences of the United States of America*, 95(3), 831–838. <https://doi.org/10.1073/pnas.95.3.831>
- Cowey, A., Small, M., & Ellis, S. (1994). Left visuo-spatial neglect can be worse in far than in near space. *Neuropsychologia*, 32(9). [https://doi.org/10.1016/0028-3932\(94\)90152-X](https://doi.org/10.1016/0028-3932(94)90152-X)
- Craig, C. M., & Lee, D. N. (1999). Neonatal control of nutritive sucking pressure: Evidence for an intrinsic τ -guide. *Experimental Brain Research*, 124(3). <https://doi.org/10.1007/s002210050634>
- Craighero, L. (2014). The role of the motor system in cognitive functions. In *The Routledge Handbook of Embodied Cognition* (pp. 51–58). doi: 10.4324/9781315775845.
- Craighero, L., Carta, A., & Fadiga, L. (2001). Peripheral oculomotor palsy affects orienting of visuospatial attention. *Neuroreport*, 12(15), 3283–3286. <https://doi.org/10.1097/00001756-200110290-00027>
- Craighero, L., Fadiga, L., Rizzolatti, G., & Umiltà, C. (1998). Visuomotor priming. *Visual Cognition*, 5(1–2), 109–125. <https://doi.org/10.1080/713756780>
- Craighero, L., Fadiga, L., Rizzolatti, G., & Umiltà, C. (1999). Action for perception: A motor-visual attentional effect. *Journal of Experimental Psychology: Human Perception and Performance*, 25(6), 1673–1692.
- Craighero, L., Fadiga, L., Umiltà, C. A., & Rizzolatti, G. (1996). Evidence for visuomotor priming effect. *Neuroreport*, 8(1), 347–349. <https://doi.org/10.1097/00001756-199612200-00068>
- Craighero, L., Ghirardi, V., Lunghi, M., Panin, F., & Simion, F. (2020). Two-day-old newborns learn to discriminate accelerated-decelerated biological kinematics from constant velocity motion. *Cognition*, 195. <https://doi.org/10.1016/j.cognition.2019.104126>
- Craighero, L., Leo, I., Umiltà, C., & Simion, F. (2011). Newborns' preference for goal-directed actions. *Cognition*, 120(1), 26–32. <https://doi.org/10.1016/j.cognition.2011.02.011>
- Craighero, L., Lunghi, M., Leo, I., Ghirardi, V., & Simion, F. (2016). Newborns' attention is driven by the translational movement. *Visual Cognition*, 24(9–10), 487–498. <https://doi.org/10.1080/13506285.2017.1322651>
- Craighero, L., & Marini, M. (2021). Implicit associations between adverbs of place and actions in the physical and digital space. *Brain Sciences*, 11(11). <https://doi.org/10.3390/brainsci11111523>
- Craighero, L., & Mele, S. (2021). Proactive gaze is present during biological and non-biological motion observation. *Cognition*, 206. <https://doi.org/10.1016/j.cognition.2020.104461>
- Craighero, L., Nascimben, M., & Fadiga, L. (2004). Eye position affects orienting of visuospatial attention. *Current Biology*, 14(4), 331–333. [https://doi.org/10.1016/S0960-9822\(04\)00051-X](https://doi.org/10.1016/S0960-9822(04)00051-X)
- Craighero, L., & Rizzolatti, G. (2005). The premotor theory of attention. *Neurobiology of Attention*. <https://doi.org/10.1016/B978-012375731-9/50035-5>
- de Vries, J. I. P., Visser, G. H. A., & Precht, H. F. R. (1982). The emergence of fetal behaviour. I. Qualitative aspects. *Early Human Development*, 7(4). [https://doi.org/10.1016/0378-3782\(82\)90033-0](https://doi.org/10.1016/0378-3782(82)90033-0)
- de Vries, J. I. P., Visser, G. H. A., & Precht, H. F. R. (1985). The emergence of fetal behaviour. II. Quantitative aspects. *Early Human Development*, 12(2). [https://doi.org/10.1016/0378-3782\(85\)90174-4](https://doi.org/10.1016/0378-3782(85)90174-4)
- DeCasper, A. J., Lecanuet, J. P., Busnel, M. C., Granier-Deferre, C., & Maugeais, R. (1994). Fetal reactions to recurrent maternal speech. *Infant Behavior and Development*, 17(2). [https://doi.org/10.1016/0163-6383\(94\)90051-5](https://doi.org/10.1016/0163-6383(94)90051-5)
- di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V., & Rizzolatti, G. (1992). Understanding motor events: A neurophysiological study. *Experimental Brain Research*, 91(1), 176–180. <https://doi.org/10.1007/BF00230027>
- Dirks, D. (1995). Bone conduction threshold testing. In J. Katz (Ed.), *Handbook of Clinical Audiology* (4th ed., pp. 132–146). Williams and Wilkins.
- Draganova, R., Eswaran, H., Murphy, P., Lowery, C., & Preissl, H. (2007). Serial magnetoencephalographic study of fetal and newborn auditory discriminative evoked responses. *Early Human Development*, 83(3). <https://doi.org/10.1016/j.earlhumdev.2006.05.018>
- Ellis, R., & Tucker, M. (2000). Micro-affordance: The potentiation of components of action by seen objects. *British Journal of Psychology*, 91(4), 451–471. <https://doi.org/10.1348/000712600161934>
- Eswaran, H., Lowery, C. L., Wilson, J. D., Murphy, P., & Preissl, H. (2004). Functional development of the visual system in human fetus using magnetoencephalography. *Experimental Neurology*, 190(SUPPL. 1). <https://doi.org/10.1016/j.expneurol.2004.04.007>
- Eswaran, H., Lowery, C. L., Wilson, J. D., Murphy, P., & Preissl, H. (2005). Fetal magnetoencephalography - A multimodal approach. *Developmental Brain Research*, 154(1). <https://doi.org/10.1016/j.devbrainres.2004.10.003>
- Eswaran, H., Preissl, H., Wilson, J. D., Murphy, P., Robinson, S. E., Rose, D., Vrba, J., & Lowery, C. L. (2002). Short-term serial magnetoencephalography recordings of fetal auditory evoked responses. *Neuroscience Letters*, 331(2). [https://doi.org/10.1016/S0304-3940\(02\)00859-5](https://doi.org/10.1016/S0304-3940(02)00859-5)
- Eswaran, H., Wilson, J. D., Preissl, H., Robinson, S. E., Vrba, J., Murphy, P., Rose, D. F., & Lowery, C. L. (2002). Magnetoencephalographic recordings of visual evoked brain activity in the human fetus. *Lancet*, 360(9335). [https://doi.org/10.1016/S0140-6736\(02\)09905-1](https://doi.org/10.1016/S0140-6736(02)09905-1)
- Eyre, J. A. (2007). Corticospinal tract development and its plasticity after perinatal injury. In *Neuroscience and Biobehavioral Reviews*, 31(8). <https://doi.org/10.1016/j.neubiorev.2007.05.011>
- Fagard, J., Esseily, R., Jacquy, L., O'Regan, K., & Somogyi, E. (2018). Fetal origin of sensorimotor behavior. *Frontiers in Neurobotics*, 12(MAY). <https://doi.org/10.3389/fnbot.2018.00023>
- Falck-Ytter, T., Greddebäck, G., & Von Hofsten, C. (2006). Infants predict other people's action goals. *Nature Neuroscience*, 9(7), 878–879. <https://doi.org/10.1038/nn1729>
- Fantz, R. L. (1964). Visual experience in infants: Decreased attention to familiar patterns relative to novel ones. *Science*, 146(3644). <https://doi.org/10.1126/science.146.3644.668>
- Farné, A., & Ladavas, E. (2000). Dynamic size-change of hand peripersonal space following tool use. *Neuroreport*, 11(8). <https://doi.org/10.1097/00001756-200006050-00010>

- Farroni, T., Massaccesi, S., Pividori, D., & Johnson, M. H. (2004). Gaze following in newborns. *Infancy*, 5(1). https://doi.org/10.1207/s15327078in0501_2
- Filippetti, M. L., Johnson, M. H., Lloyd-Fox, S., Dragovic, D., & Farroni, T. (2013). Body perception in newborns. *Current Biology*, 23(23), 2413–2416. <https://doi.org/10.1016/j.cub.2013.10.017>
- Finan, D. S., & Barlow, S. M. (1998). Intrinsic dynamics and mechanosensory modulation of non-nutritive sucking in human infants. *Early Human Development*, 52(2). [https://doi.org/10.1016/S0378-3782\(98\)00029-2](https://doi.org/10.1016/S0378-3782(98)00029-2)
- Flanagan, J. R., & Johansson, R. S. (2003). Action plans used in action observation. *Nature*, 424(6950), 769–771. <https://doi.org/10.1038/nature01861>
- Fogassi, L., Gallese, V., Fadiga, L., Luppino, G., Matelli, M., & Rizzolatti, G. (1996). Coding of peripersonal space in inferior premotor cortex (area F4). *Journal of Neurophysiology*, 76(1), 141–157. <https://doi.org/10.1152/jn.1996.76.1.141>
- Franca, M., Turella, L., Canto, R., Brunelli, N., Allione, L., Andreasi, N. G., Desantis, M., Marzoli, D., & Fadiga, L. (2012). Corticospinal facilitation during observation of graspable objects: A transcranial magnetic stimulation study. *PLoS One*, 7(11). <https://doi.org/10.1371/journal.pone.0049025>
- Freides, D. (1974). Human information processing and sensory modality: Cross-modal functions, information complexity, memory, and deficit. *Psychological Bulletin*, 81(5). <https://doi.org/10.1037/h0036331>
- Fulford, J., Vadegar, S. H., Dodampahala, S. H., Moore, R. J., Young, P., Baker, P. N., James, D. K., & Gowland, P. A. (2003). Fetal brain activity in response to a visual stimulus. *Human Brain Mapping*, 20(4). <https://doi.org/10.1002/hbm.10139>
- Gamberini, L., Carlesso, C., Seraglia, B., & Craighero, L. (2013). A behavioural experiment in virtual reality to verify the role of action function in space coding. *Visual Cognition*, 21(8), 961–969. <https://doi.org/10.1080/13506285.2013.840348>
- Gamberini, L., Seraglia, B., & Priftis, K. (2008). Processing of peripersonal and extrapersonal space using tools: Evidence from visual line bisection in real and virtual environments. *Neuropsychologia*, 46(5). <https://doi.org/10.1016/j.neuropsychologia.2007.12.016>
- Gerhardt, K. J., & Abrams, R. M. (1996). Fetal hearing: Characterization of the stimulus and response. *Seminars in Perinatology*, 20(1). [https://doi.org/10.1016/S0146-0005\(96\)80053-X](https://doi.org/10.1016/S0146-0005(96)80053-X)
- Gerhardt, K. J., Abrams, R. M., & Oliver, C. C. (1990). Sound environment of the fetal sheep. *American Journal of Obstetrics and Gynecology*, 162(1). [https://doi.org/10.1016/0002-9378\(90\)90866-6](https://doi.org/10.1016/0002-9378(90)90866-6)
- Ghio, M., Cara, C., & Tettamanti, M. (2021). The prenatal brain readiness for speech processing: A review on foetal development of auditory and primordial language networks. *Neuroscience and Biobehavioral Reviews*, 128. <https://doi.org/10.1016/j.neubiorev.2021.07.009>
- Goldberg, M. E., & Segraves, M. A. (1989). The visual and frontal cortices. In *Reviews of oculomotor research* (Vol. 3).
- Gonçalves, R. V., Figueiredo, E. M., Mourão, C. B., Colosimo, E. A., Fonseca, S. T., & Mancini, M. C. (2013). Development of infant reaching behaviors: Kinematic changes in touching and hitting. *Infant Behavior and Development*, 36(4), 825–832. <https://doi.org/10.1016/j.infbeh.2013.09.009>
- Gottlieb, G. (1971). Ontogenesis of sensory function in birds and mammals. In E. Tobach, L. R. Aronson, & E. Shaw (Eds.), *The biopsychology of development* (pp. 67–128). New York, NY: Academic Press.
- Gottlieb, G. (1976). Conceptions of prenatal development: Behavioral embryology. *Psychological Review*, 83(3). <https://doi.org/10.1037/0033-295X.83.3.215>
- Gottlieb, G. (1998). Normally occurring environmental and behavioral influences on gene activity: From central dogma to probabilistic epigenesis. *Psychological Review*, 105(4). <https://doi.org/10.1037/0033-295X.105.4.792-802>
- Grafton, S. T., Fadiga, L., Arbib, M. A., & Rizzolatti, G. (1997). Premotor cortex activation during observation and naming of familiar tools. *NeuroImage*, 6(4). <https://doi.org/10.1006/nimg.1997.0293>
- Granier-Deferre, C., Ribeiro, A., Jacquet, A. Y., & Bassereau, S. (2011). Near-term fetuses process temporal features of speech. *Developmental Science*, 14(2). <https://doi.org/10.1111/j.1467-7687.2010.00978.x>
- Graziano, M. S. A., Hu, X. T., & Gross, C. G. (1997). Coding the locations of objects in the dark. *Science*, 277(5323), 239–241. <https://doi.org/10.1126/science.277.5323.239>
- Graziano, M. S. A., Reiss, L. A. J., & Gross, C. G. (1999). A neuronal representation of the location of nearby sounds. *Nature*, 397(6718), 428–430. <https://doi.org/10.1038/17115>
- Green, J. R., & Wilson, E. M. (2006). Spontaneous facial motility in infancy: A 3D kinematic analysis. *Developmental Psychobiology*, 48(1). <https://doi.org/10.1002/dev.20112>
- Gressens, P., Rogido, M., Paindaveine, B., & Sola, A. (2002). The impact of neonatal intensive care practices on the developing brain. *Journal of Pediatrics*, 140(6). <https://doi.org/10.1067/mpd.2002.123214>
- Grèzes, J., & Decety, J. (2002). Does visual perception of object afford action? Evidence from a neuroimaging study. *Neuropsychologia*, 40(2). [https://doi.org/10.1016/S0028-3932\(01\)00089-6](https://doi.org/10.1016/S0028-3932(01)00089-6)
- Hadders-Algra, M. (2018). Early human brain development: Starring the subplate. In *Neuroscience and Biobehavioral Reviews*, 92. <https://doi.org/10.1016/j.neubiorev.2018.06.017>
- Halligan, P. W., & Marshall, J. C. (1991). Left neglect for near but not far space in man. *Nature*, 350(6318). <https://doi.org/10.1038/350498a0>
- Hardwick, R. M., Caspers, S., Eickhoff, S. B., & Swinnen, S. P. (2018). Neural correlates of action: Comparing meta-analyses of imagery, observation, and execution. In *Neuroscience and Biobehavioral Reviews*, 94. <https://doi.org/10.1016/j.neubiorev.2018.08.003>
- Hari, R. (2006). Chapter 17 Action-perception connection and the cortical mu rhythm. *Progress in Brain Research*, 159, 253–260. [https://doi.org/10.1016/S0079-6123\(06\)59017-X](https://doi.org/10.1016/S0079-6123(06)59017-X)
- Hayat, T. T. A., Nihat, A., Martinez-Biarge, M., McGuinness, A., Allsop, J. M., Hajnal, J. V., & Rutherford, M. A. (2011). Optimization and initial experience of a multiresolution balanced steady-state free precession cine sequence for the assessment of fetal behavior in utero. *American Journal of Neuroradiology*, 32(2). <https://doi.org/10.3174/ajnr.A2295>
- Hendrickson, A., & Drucker, D. (1992). The development of parafoveal and mid-peripheral human retina. *Behavioural Brain Research*, 49(1). [https://doi.org/10.1016/S0166-4328\(05\)80191-3](https://doi.org/10.1016/S0166-4328(05)80191-3)
- Hepper, P. (1995). Human fetal “olfactory” learning. *International Journal of Prenatal and Perinatal Psychology and Medicine*, 7(2).
- Hepper, P. G., Scott, D., & Shahidullah, S. (1993). Newborn and fetal response to maternal voice. *Journal of Reproductive and Infant Psychology*, 11(3). <https://doi.org/10.1080/02646839308403210>
- Hepper, P. G., & Shahidullah, B. S. (1994). Development of fetal hearing. *Archives of Disease in Childhood - Fetal and Neonatal Edition*, 71(2), F81–F87. <https://doi.org/10.1136/fn.71.2.F81>
- Hoffman, J. E., & Subramaniam, B. (1995). The role of visual attention in saccadic eye movements. *Perception & Psychophysics*, 57(6). <https://doi.org/10.3758/BF03206794>
- Hollien, H., & Feinstein, S. (1975). Contribution of the external auditory meatus to auditory sensitivity underwater. *Journal of the Acoustical Society of America*, 57(6). <https://doi.org/10.1121/1.380589>
- Hooker, D. (1952). *The prenatal origin of behavior*. University of Kansas Press.
- Huttenlocher, P. R. (1990). Morphometric study of human cerebral cortex development. *Neuropsychologia*, 28(6). [https://doi.org/10.1016/0028-3932\(90\)90031-1](https://doi.org/10.1016/0028-3932(90)90031-1)
- Iacoboni, M., Woods, R. P., Brass, M., Bekkering, H., Mazziotta, J. C., & Rizzolatti, G. (1999). Cortical mechanisms of human imitation. *In Science* (Vol., 286(5449)), 2526–2528. <https://doi.org/10.1126/science.286.5449.2526>
- James, W. (1890). *The Principles Of Psychology Volume I* By William James (1890). *The Principles of Psychology*, 1(1890), 1637.
- Jeanerod, M. (1984). The timing of natural prehension movements. *Journal of Motor Behavior*, 16(3), 235–254. <https://doi.org/10.1080/00222895.1984.10735319>
- Jékely, G., Godfrey-Smith, P., & Keijzer, F. (2021). Reafference and the origin of the self in early nervous system evolution. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 376(1821). <https://doi.org/10.1098/rstb.2019.0764>
- Johnson, S. P. (2011). Development of visual perception. *Wiley Interdisciplinary Reviews: Cognitive Science*. (Vol. 2)(5). <https://doi.org/10.1002/wcs.128>
- Jouen, F. (1988). Visual-proprioceptive control of posture in newborn infants. *Posture and gait: Development, adaptation and modulation*.
- Jouen, F., & Lepecq, J.-C. (1989). La sensibilité au flux optique chez le nouveau-né [Sensitivity to optical flow among neonates]. *Psychologie Française*, 34(1), 13–18.
- Judaš, M., Sedmak, G., & Kostović, I. (2013). The significance of the subplate for evolution and developmental plasticity of the human brain. In *Frontiers in Human Neuroscience*, (JUL) <https://doi.org/10.3389/fnhum.2013.00423>
- Kanold, P. O. (2009). Subplate neurons: Crucial regulators of cortical development and plasticity. *Frontiers in Neuroanatomy*. (Vol. 3)(AUG). <https://doi.org/10.3389/neuro.05.016.2009>
- Karmiloff-Smith, A. (1994). Beyond modularity: A developmental perspective on cognitive science. *International Journal of Language & Communication Disorders*, 29(1). <https://doi.org/10.3109/13682829409041485>
- Karrer, R., & Monti, L. A. (1995). Event-related potentials of 4–7-week-old infants in a visual recognition memory task. *Electroencephalography and Clinical Neurophysiology*, 94(6). [https://doi.org/10.1016/0013-4694\(94\)00313-A](https://doi.org/10.1016/0013-4694(94)00313-A)
- Keysers, C., Kohler, E., Umiltà, M. A., Nanetti, L., Fogassi, L., & Gallese, V. (2003). Audiovisual mirror neurons and action recognition. *Experimental Brain Research*, 153(4). <https://doi.org/10.1007/s00221-003-1603-5>
- Keysers, C., Paracampo, R., & Gazzola, V. (2018). What neuromodulation and lesion studies tell us about the function of the mirror neuron system and embodied cognition. *Current Opinion in Psychology*, 24. <https://doi.org/10.1016/j.copsyc.2018.04.001>
- Khazipov, R., & Luhmann, H. J. (2006). Early patterns of electrical activity in the developing cerebral cortex of humans and rodents. *Trends in Neurosciences*. (Vol. 29)(7). <https://doi.org/10.1016/j.tins.2006.05.007>
- Kisilevsky, B. S., Hains, S. M. J., Brown, C. A., Lee, C. T., Cowperthwaite, B., Stutzman, S. S., Swansburg, M. L., Lee, K., Xie, X., Huang, H., Ye, H. H., Zhang, K., & Wang, Z. (2009). Fetal sensitivity to properties of maternal speech and language. *Infant Behavior and Development*, 32(1). <https://doi.org/10.1016/j.infbeh.2008.10.002>
- Kisilevsky, B. S., & Low, J. A. (1998). Human Fetal Behavior: 100 Years of Study. *Developmental Review*, 18(1). <https://doi.org/10.1006/drev.1998.0452>
- Kiuchi, M., Nagata, N., Ikeno, S., & Terakawa, N. (2000). The relationship between the response to external light stimulation and behavioral states in the human fetus: How it differs from vibroacoustic stimulation. *Early Human Development*, 58(2). [https://doi.org/10.1016/S0378-3782\(00\)00074-8](https://doi.org/10.1016/S0378-3782(00)00074-8)
- Kohler, E., Keysers, C., Umiltà, M. A., Fogassi, L., Gallese, V., & Rizzolatti, G. (2002). Hearing sounds, understanding actions: Action representation in mirror neurons. *Science*, 297(5582). <https://doi.org/10.1126/science.1070311>
- Koos, B. J., & Rajae, A. (2014). Fetal breathing movements and changes at birth. *Adv. Exp. Med. Biol.*, 814. https://doi.org/10.1007/978-1-4939-1031-1_8
- Kostovic, I., & Goldman-Rakic, P. S. (1983). Transient cholinesterase staining in the mediodorsal nucleus of the thalamus and its connections in the developing human and monkey brain. *Journal of Comparative Neurology*, 219(4). <https://doi.org/10.1002/cne.902190405>
- Kostović, I., Jovanov-Milošević, N., Radoš, M., Sedmak, G., Benjak, V., Kostović-Srzić, M., Vasung, L., Čuljat, M., Radoš, M., Hüppi, P., & Judaš, M. (2014). Perinatal and early postnatal reorganization of the subplate and related cellular

- compartments in the human cerebral wall as revealed by histological and MRI approaches. *Brain Structure and Function*, 219(1). <https://doi.org/10.1007/s00429-012-0496-0>
- Kostovic, I., & Rakic, P. (1990). Developmental history of the transient subplate zone in the visual and somatosensory cortex of the macaque monkey and human brain. *Journal of Comparative Neurology*, 297(3). <https://doi.org/10.1002/cne.902970309>
- Kowler, E., Anderson, E., Doshier, B., & Blaser, E. (1995). The role of attention in the programming of saccades. *Vision Research*, 35(13). [https://doi.org/10.1016/0042-6989\(94\)00279-U](https://doi.org/10.1016/0042-6989(94)00279-U)
- Krmpotic-Nemancic, J., Kostovic, I., Kelovici, Z., Nemancic, D., & Mrzljak, L. (1983). Development of the human fetal auditory cortex: Growth of afferent fibres1. *Cells, Tissues, Organs*, 116(1). <https://doi.org/10.1159/000145727>
- Kurjak, A., Azumendi, G., Andonotopo, W., & Salihagic-Kadic, A. (2007). Three- and four-dimensional ultrasonography for the structural and functional evaluation of the fetal face. *American Journal of Obstetrics and Gynecology* (Vol. 196)(Issue 1). <https://doi.org/10.1016/j.ajog.2006.06.090>
- Kurjak, A., Azumendi, G., Vecek, N., Kupesic, S., Solak, M., Varga, D., & Chervenak, F. (2003). Fetal hand movements and facial expression in normal pregnancy studied by four-dimensional sonography. *Journal of Perinatal Medicine*, 31(6). <https://doi.org/10.1515/JPM.2003.076>
- Kurjak, A., Stanojevic, M., Andonotopo, W., Salihagic-Kadic, A., Carrera, J. M., & Azumendi, G. (2004). Behavioral pattern continuity from prenatal to postnatal life - A study by four-dimensional (4D) ultrasonography. *Journal of Perinatal Medicine*, 32(4). <https://doi.org/10.1515/JPM.2004.065>
- Kurjak, A., Tikvica, A., Stanojevic, M., Miskovic, B., Ahmed, B., Azumendi, G., & Di Renzo, G. C. (2008). The assessment of fetal neurobehavior by three-dimensional and four-dimensional ultrasound. *Journal of Maternal-Fetal and Neonatal Medicine* (Vol. 21)(Issue 10). <https://doi.org/10.1080/14767050802212166>
- Kurjak, A., Vecek, N., Hafner, T., Bozek, T., Funduk-Kurjak, B., & Ujevic, B. (2002). Prenatal diagnosis: What does four-dimensional ultrasound add? *Journal of Perinatal Medicine*, 30(1). <https://doi.org/10.1515/JPM.2002.008>
- Kustov, A. A., & Robinson, D. L. (1996). Shared neural control of attentional shifts and eye movements. *Nature*, 384(6604). <https://doi.org/10.1038/384074a0>
- Lecanuet, J.-P., & Schaal, B. (2002). Sensory performances in the human foetus : A brief summary of research. *Intellectica. Revue de l'Association Pour La Recherche Cognitive*, 34(1). <https://doi.org/10.3406/intel.2002.1072>
- Lewkowicz, D. J., & Turkewitz, G. (1980). Cross-modal equivalence in early infancy: Auditory-visual intensity matching. *Developmental Psychology*, 16(6), 597-607. <https://doi.org/10.1037/0012-1649.16.6.597>
- Libertus, K., & Needham, A. (2010). Teach to reach: The effects of active vs. passive reaching experiences on action and perception. *Vision Research*, 50(24). <https://doi.org/10.1016/j.visres.2010.09.001>
- Lickliter, R. (1990). Premature visual stimulation accelerates intersensory functioning in bobwhite quail neonates. *Developmental Psychobiology*, 23(1). <https://doi.org/10.1002/dev.420230103>
- Lickliter, R. (2000). The role of sensory stimulation in perinatal development: Insights from comparative research for care of the high-risk infant. *Journal of Developmental and Behavioral Pediatrics*, 21(6). <https://doi.org/10.1097/00004703-200012000-00007>
- Lickliter, R. (2011). The Integrated Development of Sensory Organization. In *Clinics in Perinatology* (Vol. 38, Issue 4). doi: 10.1016/j.clp.2011.08.007.
- Longo, M. R., & Lourenco, S. F. (2006). On the nature of near space: Effects of tool use and the transition to far space. *Neuropsychologia*, 44(6). <https://doi.org/10.1016/j.neuropsychologia.2005.09.003>
- Lossi, L., & Merighi, A. (2003). In vivo cellular and molecular mechanisms of neuronal apoptosis in the mammalian CNS. In *Progress in Neurobiology* (Vol. 69, Issue 5). doi: 10.1016/S0301-0082(03)00051-0.
- Lunghi, M., Piccardi, E. S., Richards, J. E., & Simion, F. (2019). The neural correlates of orienting to walking direction in 6-month-old infants: An ERP study. *Developmental Science*, 22(6). <https://doi.org/10.1111/desc.12811>
- Makris, S., Hadar, A. A., & Yarrow, K. (2011). Viewing objects and planning actions: On the potentiation of grasping behaviours by visual objects. *Brain and Cognition*, 77(2), 257-264. <https://doi.org/10.1016/j.bandc.2011.08.002>
- Maravita, A., Husain, M., Clarke, K., & Driver, J. (2001). Reaching with a tool extends visual-tactile interactions into far space: Evidence from cross-modal extinction. *Neuropsychologia*, 39(6). [https://doi.org/10.1016/S0028-3932\(00\)00150-0](https://doi.org/10.1016/S0028-3932(00)00150-0)
- Maravita, A., Spence, C., Kennett, S., & Driver, J. (2002). Tool-use changes multimodal spatial interactions between vision and touch in normal humans. *Cognition*, 83(2). [https://doi.org/10.1016/S0010-0277\(02\)00003-3](https://doi.org/10.1016/S0010-0277(02)00003-3)
- Marshall, P. J. (2016). Embodiment and human development. *Child Development Perspectives*, 10(4). <https://doi.org/10.1111/cdep.12190>
- Marshall, P. J., Houser, T. M., & Weiss, S. M. (2021). The Shared Origins of Embodiment and Development. *Frontiers in Systems Neuroscience*, 15. <https://doi.org/10.3389/fnys.2021.726403>
- Martin, A., Wiggs, C. L., Ungerleider, L. G., & Haxby, J. V. (1996). Neural correlates of category-specific knowledge. *Nature*, 379(6566). <https://doi.org/10.1038/379649a0>
- Marx, V., & Nagy, E. (2015). Fetal behavioural responses to maternal voice and touch. *PLoS One*, 10(6). <https://doi.org/10.1371/journal.pone.0129118>
- Marx, V., & Nagy, E. (2017). Fetal behavioral responses to the touch of the mother's abdomen: A frame-by-frame analysis. *Infant Behavior and Development*, 47. <https://doi.org/10.1016/j.infbeh.2017.03.005>
- Matuz, T., Govindan, R. B., Preissl, H., Siegel, E. R., Muenssinger, J., Murphy, P., Ware, M., Lowery, C. L., & Eswaran, H. (2012). Habituation of visual evoked responses in neonates and fetuses: A MEG study. *Developmental Cognitive Neuroscience*, 2(3). <https://doi.org/10.1016/j.dcn.2012.03.001>
- Maurer, D. (1993). Neonatal synesthesia: implications for the processing of speech and faces. In *Developmental neurocognition: Speech and face processing in the first year of life* (pp. 109-124). Netherlands: Springer, 10.1007/978-94-015-8234-6_10.
- Maurer, D., Gibson, L. C., & Spector, F. (2013). Synesthesia in infants and very young children. *The Oxford handbook of synesthesia (Issue December 2018)*. Oxford University Press, 10.1093/oxfordhb/9780199603329.013.0003.
- Maurer, D., & Mondloch, C. J. (2005). Neonatal Synesthesia: a Reevaluation. In *Synesthesia: Perspectives from Cognitive Neuroscience* (pp. 193-213).
- Mennella, J. A., Johnson, A., & Beauchamp, G. K. (1995). Garlic ingestion by pregnant women alters the odor of amniotic fluid. *Chemical Senses*, 20(2). <https://doi.org/10.1093/chemse/20.2.207>
- Moore, J. K., Perazzo, L. M., & Braun, A. (1995). Time course of axonal myelination in the human brainstem auditory pathway. In *Hearing Research* (Vol. 91, Issues 1-2). doi: 10.1016/0378-5955(95)00218-9.
- Murata, A., Fadiga, L., Fogassi, L., Gallese, V., Raos, V., & Rizzolatti, G. (1997). Object representation in the ventral premotor cortex (Area F5) of the monkey. *Journal of Neurophysiology*, 78(4), 2226-2230. <https://doi.org/10.1152/jn.1997.78.4.2226>
- Myowa-Yamakoshi, M., & Takeshita, H. (2006). Do human fetuses anticipate self-orientation alters the odor of amniotic fluid. *Chemical Senses*, 31(3). <https://doi.org/10.1093/chemse/31.3.207>
- Naish, K. R., Houston-Price, C., Bremner, A. J., & Holmes, N. P. (2014). Effects of action observation on corticospinal excitability: Muscle specificity, direction, and timing of the mirror response. *Neuropsychologia*, 64, 331-348. <https://doi.org/10.1016/j.neuropsychologia.2014.09.034>
- Neville, H. J. (1995). Developmental specificity in neurocognitive development in humans. In *The cognitive neurosciences*.
- Nobre, A. C., Gitelman, D. R., Dias, E. C., & Mesulam, M. M. (2000). Covert visual spatial orienting and saccades: Overlapping neural systems. *NeuroImage*, 11(3), 210-216. <https://doi.org/10.1006/nimg.2000.0539>
- Noel, J. P., Blanke, O., Magosso, E., & Serino, A. (2018). Neural adaptation accounts for the dynamic resizing of peripersonal space: Evidence from a psychophysical-computational approach. *Journal of Neurophysiology*, 119(6). <https://doi.org/10.1152/JN.00652.2017>
- Noel, J. P., Chatelle, C., Perdiks, S., Jöhr, J., Lopes Da Silva, M., Rylvlin, P., De Lucia, M., del Millán, J., del R., Diserens, K., & Serino, A. (2019). Peri-personal space encoding in patients with disorders of consciousness and cognitive-motor dissociation. *NeuroImage: Clinical*, 24. <https://doi.org/10.1016/j.nicl.2019.101940>
- Ohtaka-Maruyma, C. (2020). Subplate Neurons as an Organizer of Mammalian Neocortical Development. In *Frontiers in Neuroanatomy* (Vol. 14). <https://doi.org/10.3389/fnana.2020.00008>
- Orioli, G., Santoni, A., Dragovic, D., & Farroni, T. (2019). Identifying peripersonal space boundaries in newborns. *Scientific Reports*, 9(1). <https://doi.org/10.1038/s41598-019-45084-4>
- Parraguez, V. H., Sales, F., Valenzuela, G. J., Vergara, M., Catalán, L., & Serón-Ferré, M. (1998). Diurnal changes in light intensity inside the pregnant uterus in sheep. *Animal Reproduction Science*, 52(2), 123-130. [https://doi.org/10.1016/S0378-4320\(98\)00094-3](https://doi.org/10.1016/S0378-4320(98)00094-3)
- Paulus, M., Hunnius, S., Van Elk, M., & Bekkering, H. (2012). How learning to shake a rattle affects 8-month-old infants' perception of the rattle's sound: Electrophysiological evidence for action-effect binding in infancy. *Developmental Cognitive Neuroscience*, 2(1). <https://doi.org/10.1016/j.dcn.2011.05.006>
- Pegna, A. J., Petit, L., Caldara-Schnetzler, A. S., Khateb, A., Annoni, J. M., Sztajzel, R., & Landis, T. (2001). So near yet so far: Neglect in far or near space depends on tool use. *Annals of Neurology*, 50(6). <https://doi.org/10.1002/ana.10058>
- Piaget, J. (1952). *The Origins of Intelligence in Children. The origins of intelligence in children*. New York, NY: International Universities Press.
- Pickens, J., Field, T., Nawrocki, T., Martinez, A., Soutullo, D., & Gonzalez, J. (1994). Full-term and preterm infants' perception of face-voice synchrony. *Infant Behavior and Development*, 17(4), 447-455. [https://doi.org/10.1016/0163-6383\(94\)90036-1](https://doi.org/10.1016/0163-6383(94)90036-1)
- Poese, D., Riccio, M. L., Fagioli, M., Mazzetta, A., Fagioli, F., Parisi, P., & Fagioli, M. (2022). The newborn's reaction to light as the determinant of the brain's activation at human birth. *Frontiers in Integrative Neuroscience*, 16. <https://doi.org/10.3389/fnint.2022.933426>
- Polishuk, W. Z., Laufer, N., & Sadovsky, E. (1975). Fetal reaction to external light (Hebrew). *Harefuah*, 89(9).
- Pujol, R., Lavigne-rebillard, M., & Uziel, A. (1991). Development of the human cochlea. *Acta Oto-Laryngologica*, 111(S482). <https://doi.org/10.3109/00016489109128023>
- Quadrelli, E., Roberti, E., Turati, C., & Craighero, L. (2019). Observation of the point-light animation of a grasping hand activates sensorimotor cortex in nine-month-old infants. *Cortex*, 119. <https://doi.org/10.1016/j.cortex.2019.07.006>
- Querleu, D., Renard, X., Boutteville, C., & Crepin, G. (1989). Hearing by the human fetus? In *Seminars in Perinatology* (Vol. 13, Issue 5).
- Rabinowicz, T., De Courten-Myers, G. M., Petetot, J. M. C., Xi, G., & De Los Reyes, E. (1996). Human cortex development: Estimates of neuronal numbers indicate major loss late during gestation. *Journal of Neuropathology and Experimental Neurology*, 55(3). <https://doi.org/10.1097/00005072-199603000-00007>
- Reid, V. M., Dunn, K., Young, R. J., Amu, J., Donovan, T., & Reissland, N. (2017). The human fetus preferentially engages with face-like visual stimuli. *Current Biology*, 27(12). <https://doi.org/10.1016/j.cub.2017.05.044>
- Reissland, N., Francis, B., Aydin, E., Mason, J., & Schaal, B. (2014). The development of anticipation in the fetus: A longitudinal account of human fetal mouth movements in reaction to and anticipation of touch. *Developmental Psychobiology*, 56(5). <https://doi.org/10.1002/dev.21172>
- Reissland, N., Francis, B., Mason, J., & Lincoln, K. (2011). Do facial expressions develop before birth? *PLoS One*, 6(8). <https://doi.org/10.1371/journal.pone.0024081>

- Reynolds, G. D., Courage, M. L., & Richards, J. E. (2010). Infant attention and visual preferences: Converging evidence from behavior, event-related potentials, and cortical source localization. *Developmental Psychology*, 46(4). <https://doi.org/10.1037/a0019670>
- Reynolds, G. D., & Richards, J. E. (2009). Cortical source localization of infant cognition. *In Developmental Neuropsychology*, 34(Issue 3). <https://doi.org/10.1080/87565640902801890>
- Richards, D. S., Frentzen, B., Gerhardt, K. J., McCann, M. E., & Abrams, R. M. (1992). Sound levels in the human uterus. *Obstetrics and Gynecology*, 80(2).
- Rizzolatti, G. (1983). Mechanisms of Selective Attention in Mammals. *In Advances in Vertebrate Neuroethology*. https://doi.org/10.1007/978-1-4684-4412-4_12
- Rizzolatti, G., Camarda, R., Fogassi, L., Gentilucci, M., Luppino, G., & Matelli, M. (1988). Functional organization of inferior area 6 in the macaque monkey - II. Area F5 and the control of distal movements. *Experimental Brain Research*, 71(3), 491–507. <https://doi.org/10.1007/BF00248742>
- Rizzolatti, G., & Craighero, L. (1998). *Spatial attention: Mechanisms and theories* (pp. 171–198).
- Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annual Review of Neuroscience*, 27(1), 169–192. <https://doi.org/10.1146/annurev.neuro.27.070203.144230>
- Rizzolatti, G., Fogassi, L., & Gallese, V. (2001). Neurophysiological mechanisms underlying the understanding and imitation of action. *Nature Reviews Neuroscience*, 2(9), 661–670. <https://doi.org/10.1038/35090060>
- Rizzolatti, G., Riggio, L., Dascola, I., & Umiltà, C. (1987). Reorienting attention across the horizontal and vertical meridians: Evidence in favor of a premotor theory of attention. *Neuropsychologia*, 25(1 PART 1), 31–40. [https://doi.org/10.1016/0028-3932\(87\)90041-8](https://doi.org/10.1016/0028-3932(87)90041-8)
- Ronga, I., Galigani, M., Bruno, V., Noel, J.-P., Gazzini, A., Perathoner, C., Serino, A., & Garbarini, F. (2021). Spatial tuning of electrophysiological responses to multisensory stimuli reveals a primitive coding of the body boundaries in newborns. *Proceedings of the National Academy of Sciences*, 118(12). <https://doi.org/10.1073/pnas.2024548118>
- Roodenrys, P. J., Wladimiroff, J. W., van Es, A., & Prechtl, H. F. R. (1991). Classification and quantitative aspects of fetal movements during the second half of normal pregnancy. *Early Human Development*, 25(1). [https://doi.org/10.1016/0378-3782\(91\)90203-F](https://doi.org/10.1016/0378-3782(91)90203-F)
- Rotman, G., Troje, N. F., Johansson, R. S., & Flanagan, J. R. (2006). Eye movements when observing predictable and unpredictable actions. *Journal of Neurophysiology*, 96(3), 1358–1369. <https://doi.org/10.1152/jn.00227.2006>
- Rousseau, J.-J. (1762). *Emile ou de l'éducation*. Nœuleme.
- Sato, M., Kanenishi, K., Hanaoka, U., Noguchi, J., Marumo, G., & Hata, T. (2014). 4D ultrasound study of fetal facial expressions at 20–24 weeks of gestation. *International Journal of Gynecology and Obstetrics*, 126(3). <https://doi.org/10.1016/j.ijgo.2014.03.036>
- Schaal, B., Marlier, L., & Soussignan, R. (2000). Human foetuses learn odours from their pregnant mother's diet. *Chemical Senses*, 25(6). <https://doi.org/10.1093/chemse/25.6.729>
- Sekulić, S. R., Lukačić, D. D., & Naumović, N. M. (2005). The fetus cannot exercise like an astronaut: Gravity loading is necessary for the physiological development during second half of pregnancy. *Medical Hypotheses*, 64(2). <https://doi.org/10.1016/j.mehy.2004.08.012>
- Shahidullah, S., & Hepper, P. G. (1994). Frequency discrimination by the fetus. *Early Human Development*, 36(1). [https://doi.org/10.1016/0378-3782\(94\)90029-9](https://doi.org/10.1016/0378-3782(94)90029-9)
- Shatz, C. J. (1992). The developing brain. *Scientific American*, 267(3), 60–67. <https://doi.org/10.1038/scientificamerican0992-60>
- Sheridan, C. J., Preissl, H., Siegel, E. R., Murphy, P., Ware, M., Lowery, C. L., & Eswaran, H. (2008). Neonatal and fetal response decrement of evoked responses: A MEG study. *Clinical Neurophysiology*, 119(4). <https://doi.org/10.1016/j.clinph.2007.11.174>
- Sheridana, C. J., Matuz, T., Draganova, R., Eswaran, H., & Preissla, H. (2010). Fetal Magnetoencephalography- achievements and challenges in the study of prenatal and early postnatal brain responses: A review. *Infant and Child Development*, 19(1). <https://doi.org/10.1002/icd.657>
- Simner, J. (2012). Defining synaesthesia. *British Journal of Psychology*, 103(1). <https://doi.org/10.1348/000712610X528305>
- Slater, A. M. (2002). Visual perception in the newborn infant : Issues and debates. *Intellectica. Revue de l'Association Pour La Recherche Cognitive*, 34(1). <https://doi.org/10.3406/intel.2002.1073>
- Smotherman, W. P., Robinson, S. R., Ronca, A. E., Alberts, J. R., & Hepper, P. G. (1991). Heart rate response of the rat fetus and neonate to a chemosensory stimulus. *Physiology and Behavior*, 50(1). [https://doi.org/10.1016/0031-9384\(91\)90496-B](https://doi.org/10.1016/0031-9384(91)90496-B)
- Smyth, C. N. (1965). Experimental methods for testing the integrity of the fetus and neonate. *J Obstet Gynaecol Br Commun*, 72, 920.
- Southgate, V., Johnson, M. H., Osborne, T., & Csibra, G. (2009). Predictive motor activation during action observation in human infants. *Biology Letters*, 5(6), 769–772. <https://doi.org/10.1098/rsbl.2009.0474>
- Spahn, J. M., Callahan, E. H., Spill, M. K., Wong, Y. P., Benjamin-Neelon, S. E., Birch, L., Black, M. M., Cook, J. T., Faith, M. S., Mennella, J. A., & Casavale, K. O. (2019). Influence of maternal diet on flavor transfer to amniotic fluid and breast milk and children's responses: A systematic review. *In American Journal of Clinical Nutrition*, 109. <https://doi.org/10.1093/ajcn/nqy240>
- Sparling, J. W., Van Tol, J., & Chescheir, N. C. (1999). Fetal and neonatal hand movement. *Physical Therapy*, 79(1). <https://doi.org/10.1093/ptj/79.1.24>
- Sparling, J. W., & Wilhelm, I. J. (1993). Quantitative measurement of fetal movement: Fetal-post and movement assessment (f-PAM). *Physical and Occupational Therapy in Pediatrics*, 12(2–3), 97–114. https://doi.org/10.1080/J006v12n02_06
- Stiles, J. (2009). On genes, brains, and behavior: Why should developmental psychologists care about brain development? *Child Development Perspectives*, 3(3). <https://doi.org/10.1111/j.1750-8606.2009.00106.x>
- Streri, A., & de Hevia, M. D. (2023). How do human newborns come to understand the multimodal environment? *Psychonomic Bulletin and Review*, 30(4). <https://doi.org/10.3758/s13423-023-02260-y>
- Streri, A., & Gentaz, E. (2004). Cross-modal recognition of shape from hand to eyes and handedness in human newborns. *Neuropsychologia*, 42(10), 1365–1369. <https://doi.org/10.1016/j.neuropsychologia.2004.02.012>
- Streri, A., & Pêcheux, M.-G. (1986). Vision-to-touching and touch-to-vision transfer of form in 5-month-old infants. *British Journal of Developmental Psychology*, 4(2). <https://doi.org/10.1111/j.2044-835x.1986.tb01007.x>
- Syme, M. R., Paxton, J. W., & Keelan, J. A. (2004). Drug transfer and metabolism by the human placenta. *Clinical Pharmacokinetics*, 43(Issue 8). <https://doi.org/10.2165/00003088-200443080-00001>
- Symes, E., Ellis, R., & Tucker, M. (2007). Visual object affordances: Object orientation. *Acta Psychologica*, 124(2), 238–255. <https://doi.org/10.1016/j.actpsy.2006.03.005>
- Thomas, B. L., Karl, J. M., & Whishaw, I. Q. (2014). Independent development of the Reach and the Grasp in spontaneous self-touching by human infants in the first 6 months. *Frontiers in Psychology*, 5(OCT). <https://doi.org/10.3389/fpsyg.2014.01526>
- Tucker, M., & Ellis, R. (1998). On the Relations between Seen Objects and Components of Potential Actions. *Journal of Experimental Psychology: Human Perception and Performance*, 24(3), 830–846. <https://doi.org/10.1037/0096-1523.24.3.830>
- Turati, C., Simion, F., Milani, I., & Umiltà, C. (2002). Newborns' preference for faces: What is crucial? *Developmental Psychology*, 38(6). <https://doi.org/10.1037/0012-1649.38.6.875>
- Turkewitz, G., & Kenny, P. A. (1985). The role of developmental limitations of sensory input on sensory/perceptual organization. *Journal of Developmental and Behavioral Pediatrics*, 6(5). <https://doi.org/10.1097/00004703-198510000-00014>
- Turvey, M. T., & Fonseca, S. T. (2014). The medium of haptic perception: A tensegrity hypothesis. *Journal of Motor Behavior*, 46(3). <https://doi.org/10.1080/00222895.2013.798252>
- Ustun, B., Reissland, N., Covey, J., Schaal, B., & Blissett, J. (2022). Flavor sensing in utero and emerging discriminative behaviors in the human fetus. *Psychological Science*, 33(10), 1651–1663. <https://doi.org/10.1177/09567976221105460>
- Valenza, E., Simion, F., Cassia, V. M., & Umiltà, C. (1996). Face Preference at Birth. *Journal of Experimental Psychology: Human Perception and Performance*, 22(4). <https://doi.org/10.1037/0096-1523.22.4.892>
- Van Der Meer, A. L. (1997). Keeping the arm in the limelight: Advanced visual control of arm movements in neonates. *European Journal of Paediatric Neurology*, 1(4). [https://doi.org/10.1016/S1090-3798\(97\)80040-2](https://doi.org/10.1016/S1090-3798(97)80040-2)
- Vanderwert, R. E., Fox, N. A., & Ferrari, P. F. (2013). The mirror mechanism and mu rhythm in social development. *Neuroscience Letters*, 540, 15–20. <https://doi.org/10.1016/j.neulet.2012.10.006>
- F.J. Varela, E. Thompson, E. Rosch, J. Kabat-Zinn The embodied mind: Cognitive science and human experience 2016 The Embodied Mind: Cognitive Science and Human Experience. 10.29173/cmplct8718.
- Vasung, L., Abaci Turk, E., Ferradal, S. L., Sutin, J., Stout, J. N., Ahtam, B., Lin, P. Y., & Grant, P. E. (2019). Exploring early human brain development with structural and physiological neuroimaging. *NeuroImage*, 187. <https://doi.org/10.1016/j.neuroimage.2018.07.041>
- Vasung, L., Jovanov-Milošević, N., Pletikos, M., Mori, S., Judaš, M., & Kostovi, I. (2011). Prominent periventricular fiber system related to ganglionic eminence and striatum in the human fetal cerebrum. *Brain Structure and Function*, 215(3–4). <https://doi.org/10.1007/s00429-010-0279-4>
- Versace, E., Damini, S., & Stancher, G. (2020). Early preference for face-like stimuli in solitary species as revealed by tortoise hatchlings. *Proceedings of the National Academy of Sciences of the United States of America*, 117(39). <https://doi.org/10.1073/pnas.2011453117>
- von Hofsten, C. (1982). Eye-hand coordination in the newborn. *Developmental Psychology*, 18(3). <https://doi.org/10.1037/0012-1649.18.3.450>
- von Hofsten, C. (2009). Action, the foundation for cognitive development. *Scandinavian Journal of Psychology*, 50(6), 617–623. <https://doi.org/10.1111/j.1467-9450.2009.00780.x>
- Ward, J. (2013). Synesthesia. *Annual Review of Psychology*, 64(1), 49–75. <https://doi.org/10.1146/annurev-psych-113011-143840>
- Wilson, E. K. (2014). Ex Utero: Live human fetal research and the films of Davenport Hooker. *Bulletin of the History of Medicine*, 88(1). <https://doi.org/10.1353/bhm.2014.0002>
- Witt, M. (2020). *Anatomy and development of the human gustatory and olfactory systems. The Senses: A Comprehensive Reference*, 10.1016/b978-0-12-809324-5.24204-1.
- Witt, M., & Reutter, K. (1998). Innervation of developing human taste buds. An immunohistochemical study. *Histochemistry and Cell Biology*, 109(3). <https://doi.org/10.1007/s004180050228>
- Xie, W., & Richards, J. E. (2017). The relation between infant covert orienting, sustained attention and brain activity. *Brain Topography*, 30(2), 198–219. <https://doi.org/10.1007/s10548-016-0505-3>
- Zappasodi, F., Tecchio, F., Pizzella, V., Cassetta, E., Romano, G. V., Filligoi, G., & Rossini, P. M. (2001). Detection of fetal auditory evoked responses by means of

- magnetoencephalography. *Brain Research*, 917(2). [https://doi.org/10.1016/S0006-8993\(01\)02901-8](https://doi.org/10.1016/S0006-8993(01)02901-8)
- Zoia, S., Blason, L., D'Ottavio, G., Biancotto, M., Bulgheroni, M., & Castiello, U. (2013). The development of upper limb movements: From fetal to post-natal life. *PLoS One*, 8(12). <https://doi.org/10.1371/journal.pone.0080876>
- Zoia, S., Blason, L., D'Ottavio, G., Bulgheroni, M., Pezzetta, E., Scabar, A., & Castiello, U. (2007). Evidence of early development of action planning in the human foetus: A kinematic study. *Experimental Brain Research*, 176(2), 217–226. <https://doi.org/10.1007/s00221-006-0607-3>