

Neonatal imitation in context: Sensorimotor development in the perinatal period

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Abstract: More than 35 years ago, Meltzoff and Moore (1977) published their famous article, “Imitation of facial and manual gestures by human neonates.” Their central conclusion, that neonates can imitate, was and continues to be controversial. Here, we focus on an often-neglected aspect of this debate, namely, neonatal spontaneous behaviors themselves. We present a case study of a paradigmatic orofacial “gesture,” namely tongue protrusion and retraction (TP/R). Against the background of new research on mammalian aerodigestive development, we ask: How does the human aerodigestive system develop, and what role does TP/R play in the neonate’s emerging system of aerodigestion? We show that mammalian aerodigestion develops in two phases: (1) from the onset of isolated orofacial movements *in utero* to the postnatal mastery of suckling at 4 months after birth; and (2) thereafter, from preparation to the mastery of mastication and deglutition of solid foods. Like other orofacial stereotypies, TP/R emerges in the first phase and vanishes prior to the second. Based upon recent advances in activity-driven early neural development, we suggest a sequence of three developmental events in which TP/R might participate: the acquisition of tongue control, the integration of the central pattern generator (CPG) for TP/R with other aerodigestive CPGs, and the formation of connections within the cortical maps of S1 and M1. If correct, orofacial stereotypies are crucial to the maturation of aerodigestion in the neonatal period but also unlikely to co-occur with imitative behavior.

Keywords: activity-dependent neural development; aerodigestion; imitation; neonatal behaviour; perinatal development; stereotypy

1. Introduction

A growing body of contemporary research in child development is motivated by the insight that we must pay attention to the concrete motor mechanisms of the developing infant or risk incorrect interpretation of infant behaviour. Esther Thelen’s work on newborn stepping is perhaps the best-known example. Thelen and her colleagues examined a host of component systems that appeared relevant to infant stepping. This led to the striking discovery that the disappearance of stepping movements in the second or third month is not a result of the cortical inhibition of a “stepping mechanism” but to the disproportionate growth of leg muscles and fat tissue. When infants’ legs are submerged in water to alleviate the effects of gravity, non-stepping infants resumed stepping behaviour (Thelen et al. 1984). Infants also showed alternating stepping patterns on a treadmill long before they began walking independently (Thelen & Ulrich 1991). Similar in-depth treatments of specific action systems such as looking, crawling, reaching, object manipulation, postural adjustment, and locomotion reveal the crucial role of the motor systems in the development of perception and cognition (e.g., Adolph

1997; Bushnell & Boudreau 1993; Campos et al. 2000; Freedland & Bertenthal 1994; Gibson & Schumuckler 1989; Thelen et al. 2001; von Hofsten 1989).

Here we contribute to this general line of research by looking at neonatal imitation through the lens of perinatal sensorimotor development. Despite nearly four decades of research on neonatal imitation and the incredible controversy it has generated, psychologists (as opposed to pediatric neurologists) have spent very little time investigating neonatal rhythmic motor behaviour, that is, the very “gestures” tested for imitation in neonate imitation experiments. To remedy this void, we present a theory of aerodigestive development and argue that the standard orofacial “gestures” used in imitation experiments are in fact *aerodigestive stereotypies*, a set of rhythmic motor sequences that emerge as the first structured behaviours in human/mammalian gestation. We explain the crucial role that stereotypies play in the perinatal aerodigestive development and why the positive results of neonatal imitation experiments should be re-examined in light of these developmental processes.

Note that this article is not intended as a review, meta-analysis, or formal critique of the experimental methods

used in neonatal imitation research. Nor do we attempt to resolve the many tangled issues that have arisen over 40 years of debate. (There are a number of articles of this kind, e.g., Anisfeld 1991; 1996; 2005; Oostenbroek et al. 2013; Ray & Heyes 2011). Instead, we present a case study of a paradigmatic “gesture,” *tongue protrusion and retraction* (hereafter TP/R), and argue that our results are generalizable and applicable, *mutatis mutandis*, to other tested gestures. There are several reasons for our choice. First, insofar as there is any agreement between the skeptics and proponents, everyone agrees that TP/R has garnered the most robust data: If neonates imitate *any* gesture, then TP/R is that gesture. Second, in the past decade there has been a surge of interest in neurophysiological studies of perinatal aerodigestive behaviours in mammals (e.g., in rats and pigs). Imaging studies on human infants have served to bridge the gap between these mammalian experiments and the human case. It is therefore possible to tell a developmental story – albeit sometimes a sketchy story – about the role of TP/R in motor development. Third, as we will argue, TP/R is merely one of many infant stereotypies present at birth. In our view, therefore, the story of TP/R development is representative of the other rhythmic movements commonly tested in neonatal imitation experiments, orofacial or otherwise. In some deep sense, then, this article is not about TP/R per se. It’s about the role of rhythmic behaviours in neural development, about why we need to look “under the hood” in addition to doing careful behavioural work.

2. The neonatal imitation controversy

Over a century ago, Edward Thorndike (1898) pointed out that imitation, which he famously defined as “learning to do an act from seeing it done,” is not a psychologically trivial feat. To imitate another person’s behaviour, you must *visually parse* the actions to be imitated, *translate* them (as parsed) into the first-person point of view, and possess the *motor expertise* to realize those goals. Opaque imitation – when the imitator cannot observe and compare his or her own movements to the target – is especially challeng-

ing. It is notoriously difficult to gain a fine-grained, real-time understanding of one’s own bodily movements with proprioception as the only source of feedback. This is why dance studios have mirrors and swim coaches use aquatic cameras. It was thus believed that infants could not imitate opaque gestures until the age of 8–12 months. Of course, infants could engage in contagious crying or the mimicry of emotional expressions prior to the age of 8–12 months, but considerable prior multimodal experience is required for opaque imitation (Piaget 1962).

Meltzoff and Moore’s (1977) paper thus reported a remarkable finding: Neonates can copy the orofacial gestures of tongue protrusion, mouth opening, and lip pursing – three types of opaque imitation – as well as match sequential finger movements. When infants were shown these gestures, they responded in kind, producing the modeled gesture more often than an unrelated one. For example, an infant who viewed a demonstration of tongue protrusion responded more frequently with tongue protrusion than with mouth opening. The authors argued that these results could not be explained in terms of reflexes, releasing mechanisms, or simple resonance mechanisms. Instead, given the number of gestures imitated (i.e., that passed this operational definition of imitation) plus the variation in the execution of each imitated gesture, Meltzoff and Moore argued that infants must have a common supramodal system of action representation, one that converts the neonate’s visual representations of observed action into proprioceptive space, thence from proprioceptive space into motor commands. This hypothesis became known as the theory of *active intermodal matching* (AIM) that Meltzoff and Moore (1983; 1985; 1989; 1992; 1994) then refined with further experiments. According to the robust theory, neonatal imitation was (a) generative (displaying both variety and novelty); (b) self-correcting (aiming at an accurate performance); (c) specific to occurrent movement such as the duration of the gesture (not simply the activated “organ”); and (d) temporally flexible (executed by memory after a delay and in the absence of any stimulus).

The current definition of imitation in experimental psychology no longer confines imitation to actions that we *see*. A comic can mimic a politician’s speech in both voice and gesture; adults can learn American Sign Language with only haptic guidance. Nor do most psychologists believe that imitation must involve conscious intent or the perception of the target behaviour as an intentional action by the actor. A young child imitates his father when he unconsciously mirrors his gait; a toddler parrots her mother’s telephone manner without knowing what her mother said (Brass & Heyes 2005; Hata et al. 2009). Thus, the modern definition of imitation highlights what cognitive neuroscientists have called “the correspondence problem” – the problem of determining, on the basis of observation, what sequence of motor commands will reproduce the observed behaviours. This broadening of the definition makes the existence of neonatal imitation more plausible: Neonates need not know that they are imitating, nor understand what they imitate, nor intend to imitate the actions of others.

Despite this revision, neonatal imitation remains controversial. (For an unbiased recent review of the debate, see Oostenbroek et al. 2013). Detractors have questioned – and continue to question – the reproducibility of the early results and the standard experimental methodology inclusive of data collection and analysis (Abravanel & Sigafos

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1984; Anisfeld 1991; 1996; 2005; Anisfeld et al. 2001). They point to the short timeline of neonatal imitation and the odd phenomenon of imitation “drop out.” At birth, human neonates produce multiple orofacial gestures both spontaneously and when adults model those behaviours. By 6 weeks after birth, however, these behaviours have markedly diminished; by 3 months they are almost entirely absent (Abravanel & Sigafos 1984; Fontaine 1984; Heimann et al. 1989; Jacobson 1979; Kugiumutzakis 1999). These facts are mirrored in the nonhuman primate world. Chimpanzees no longer imitate 8 weeks postpartum (Myowa-Yamakoshi et al. 2004), and macaques appear to imitate human facial expressions on only one day, postpartum Day 3 (Ferrari et al. 2006b). Whatever role (if any) these short-lived orofacial gestures play, they are unlikely to be the developmental precursors of later imitation skills in infants. Detractors also point to a recent meta-analysis of the neonate imitation research papers (Ray & Heyes 2011) that claims that only one type of gesture, TP, has garnered more positive than negative results overall. Of course, detractors must provide an alternative explanation of such results that resist “explaining away.” To date, these alternative explanations fall into roughly two classes (with apologies to outliers): What we see is explained by neonatal reflexes triggered by releasing mechanisms (Jacobson 1979) and/or by systemic factors in neonatal development, such as arousal (Anisfeld 1991; 1996; 2005; Jones 1996; 2006a; 2006b).

On the other side of the debate, proponents of neonatal imitation are satisfied that Meltzoff and Moore’s original results have been largely replicated (Heimann et al. 1989; Kugiumutzakis 1999; Legerstee 1991; Vinter 1986) and even extended to some new gestures (e.g., hand opening and closing [Vinter 1986]; blinking [Kugiumutzakis 1999]; lateral head motion [Meltzoff & Moore 1989]; and emotional expressions [Field 1982; 1983]). Like AIM detractors, proponents must explain the experimental results: why and how neonates imitate adults (in the ways they do) at such an early stage of development/experience. Here, social explanations are common. Proponents argue that neonatal imitation is an evolved mechanism that promotes maternal/caregiver attachment to the newborn, a trait essential to infant survival given the physiological immaturity of our species at birth. This is why proponents view neonatal imitation (NI) experiments on nonhuman primates as corroboration for the theory: If NI promotes infant survival we should see the same behaviours in other nonhuman primates with similar social structure, state of maturation at birth, and communicative gestures. Proponents must also address the phenomenon of imitation drop out—that is, deny its existence or explain its purpose/origins. Here, most proponents follow Meltzoff and Moore’s (1992) explanation: Drop-out is a sign of the infant’s changing social and cognitive inclinations. By three months of age the infant has moved on to other forms of social interaction such as gaze-sharing and vocalization and, thus, no longer finds the imitation of basic facial gestures socially useful. In other words, drop-out results from a change in *performance* not competence, as the later emergence of sophisticated imitation makes clear. Finally, proponents have been buoyed by a competing meta-analysis of the data, Simpson et al.’s (2014a), which showed that 85% of all tests for neonatal imitation have yielded positive results

if one includes both human and “primate-other” data and excludes infants older than 28 days of age and experiments with small sample sizes.

Despite the continuing controversy, Meltzoff and Moore’s early papers are among the most widely disseminated results in 20th century psychology. Researchers in psychology, philosophy, linguistics, neurophysiology, and comparative ethology have integrated Meltzoff and Moore’s findings into their theories, often as a theoretical cornerstone. Such theories span a wide range of subjects from the mental capacities of Old and New World primates to the individual development of empathy, language, the sense of self, and our theory of mind (Bard 2007; Bermudez 2000; Champoux et al. 2009; Gallagher 2005; Gallagher & Meltzoff 1996; Gallese 2005; Go et al. 2008; Goldman 2006; Gopnik et al. 1999; Gopnik & Wellman 1992; Kuhl 2000; Metzinger 2004; Myowa 1996; Myowa-Yamakoshi et al. 2004; Preston & de Waal 2002; Trevarthen & Aitken 2001).

More recently, neonatal imitation has garnered renewed interest in the wake of the discovery of mirror neurons in the premotor cortex of macaques (Rizzolatti et al. 1996). These theories suggest that mirror neurons are the building blocks of a host of core human traits including language (D’Ausilio et al. 2009), empathy (Gallese 2003; Leslie et al. 2004), theory of mind (Meltzoff & Decety 2003), and imitation (Iacoboni 2009a). Interestingly, the neonatal imitation experiments provide the *only* evidence that mirror neurons are present at birth, and thus are part of an innate system of action perception (Gallese 2003; Iacoboni et al. 1999, 2005; Lepage & Théoret 2007; Meltzoff & Decety 2003; Nagy & Molnar 2004). The assumption that neonatal imitation exists is well entrenched in contemporary cognitive science despite a lack of resolution to the controversy.

In what follows, we offer an explanation of neonatal imitation in terms of the development of mammalian/human aerodigestion. Section 3 presents an overview of human aerodigestive function and the problems inherent in a dual system for respiration and suckling/swallowing, facts necessary to understand why mammalian aerodigestion develops as it does. In section 4, we arrive at aerodigestive development itself. Here we focus on the role of TP/R in both prenatal and postnatal development. Although aerodigestion is the first complex sensorimotor system to develop, only a rudimentary system exists at birth. With access to air and the onset of suckling, the infant’s system gains expertise through practice. During this learning period, a series of failsafe mechanisms protect the novice system from accident. In these first postnatal months, however, the anatomy of the system gradually transforms from a system well suited to suckling and respiration to one that can masticate, manipulate, and swallow solid food while continuing to breathe. We argue that if one lines up the milestones of perinatal aerodigestion presented in section 3 with the appearance and extinction of TP/R, TP/R shows lock-step timing with this first phase of development. This is unlikely to be a coincidence. In section 5 we then argue that TP/R is an aerodigestive stereotypy, one of many such behaviours present in the perinatal infant. Section 6 begins with an introduction to some recent work on rhythmic behaviours and neural development. Using this background, we present a series of neurodevelopmental events to which TP/R is likely to contribute. Listed in developmental order, those are (1) the acquisition of tongue control; (2) the integration of the central pattern

generator (CPG) for TP/R with other aerodigestive CPGs; and (3) the formation of connections within the cortical maps of S1 and M1. Finally, in section 7, we return to Meltzoff and Moore's original experiments. We show why, on the balance of evidence, that the positive experimental results for *any* of the stereotypies tested in human and nonhuman primates – indeed for any mammal – are unlikely to be best explained by imitation. We conclude with brief remarks about how a more integrative and interdisciplinary perspective could benefit developmental psychology.

3. Human aerodigestive function

3.1. Aerodigestion: A dual system

As the name suggests, the mammalian aero-digestive tract serves two central functions: respiration and digestion. In all mammals except adult chimpanzees and humans (Nishimura et al. 2008), the basic structure consists of two tubes that cross, forming an X. At this juncture the four-way intersection is open to both systems. In chimpanzees and humans, however, postnatal growth adds a short connecting tube, the laryngopharynx, between the upper and lower branches of both systems, shared by both respiratory and digestive systems (Lieberman et al. 2001; Nishimura 2003; Nishimura et al. 2003).

The primary problem of the dual system is ensuring that the right stuff ends up in the right place – air in the lungs and fluids/saliva/masticated food in the stomach. Ideally, air is inhaled up through the nostrils, into the nasal cavities, and then passes back down into the pharynx, through the lens-shaped opening of the larynx (the glottis), into the trachea and down into the lungs (Fig. 1). In digestion, liquids or solid food should be drawn into the mouth/oral cavity by the lips, pushed into the oropharynx by the tongue, travel down the laryngopharynx by peristalsis, then into the esophagus, and finally into the stomach (Dodds 1989; Palmer et al. 1992; Thexton 1992; Thexton & Crompton 1998). As with any dual system, this shared real estate (the laryngopharynx) necessitates a protocol for usage – “when is it yours and when is it mine”? In aerodigestion, two additional complications arise. First, neither the digestive nor the respiratory tract is a physiologically dedicated pathway for the intake of nutrition and air respectively: Adults can inhale through the mouth, and the digestive tract also serves to drain the nasal cavities. Second, both aerodigestive paths must be capable of *two-way flow*. In respiration, we breathe in and out. In digestion, the stomach is filled by ingestion and on occasion, emptied by emesis.

This “open” arrangement of the dual system combined with the passage of fluids and gases through both tracts creates ample opportunity for mishap. Saliva and fluid from the nasal cavities amount to more than two liters of fluid per day. If misdirected into the lungs, this is enough liquid to cause suffocation within 24 hours. So “non-nutritive swallowing” is one of the pharynx's most vital functions. Aspiration of fluids is also a serious problem. Here, the shared laryngopharynx carries the risk of aspiration pneumonia during feeding (Kohda et al. 1994). This risk is so serious that it appears to have acted as a strong constraint on the evolution of the aerodigestive system: Clearing the pharynx of fluids or food takes precedence over *all*

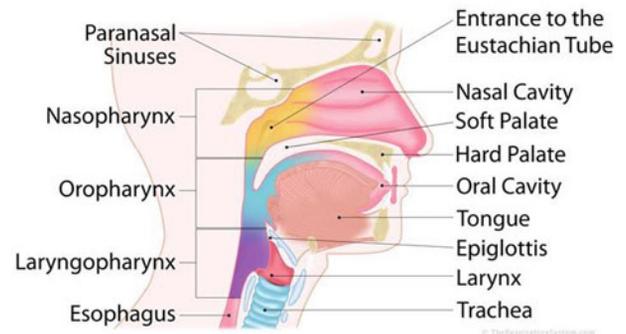


Figure 1. A detailed anatomy of the aerodigestive system.

competing functions, including respiration (Broussard & Altschuler 2000). Exhalation and emesis have their own risks, however. Exhalation during swallow can cause fluid to be forced into the sinuses and out the nasal cavities (as anyone who starts to laugh while drinking knows too well). For neonates, who have a prodigious capacity for emesis, repeated “mistakes” of this kind can lead to infection of the sinuses and the inner ear, via the Eustachian tubes.

The general solution to these problems is a set of functionally interconnected “valves”¹ that open and close the passages of ingress and egress. Two sphincters control ingress to and egress from the lower aerodigestive system: The entire larynx – epiglottis, aryepiglottic folds, ventricular folds, and vocal folds – protect the airway; the upper esophageal sphincter allows food and liquid into the esophagus. Yet another valve, the lower esophageal sphincter, controls flow into and out of the stomach itself. At the top of the aerodigestive system, the nasal cavities are sealed by the soft palate that moves backwards to contact the pharyngeal wall. In adults, the lips and posterior tongue also do double duty as aerodigestive “valves”: Lips prevent liquids from escaping from the mouth, and at the back of the oral cavity, the posterior tongue blocks entry into the oropharynx (Fig. 1). At the same time, the anterior tongue prevents the accidental re-entrance of the bolus into the mouth. In between these points of closure, sets of muscles control the movement of solids, fluids, and gases either via peristaltic motion (a wave-like motion of serial muscle groups) or by the differences in air pressure.

In sum, the tongue plays a pivotal role in human aerodigestion. In the adult, it serves to shift food about for mastication, and to form and hold a liquid or solid bolus within the mouth until swallowing. During swallowing, it blocks re-entry to the mouth and acts as an airlock to the nasal cavities, preventing the exhalation of liquids into those cavities. Even in the infant, tongue behaviour must be coordinated with respiration, jaw movement, epiglottal closure, and the peristaltic movements of pharynx – all sensorimotor events of great complexity.

3.2. The goal: Aerodigestion at birth

At birth, aerodigestive control is the human infant's most complex sensorimotor capacity. Even the “simple” or pharyngeal swallow requires the co-ordination of 26 pairs of muscles, inputs from five cranial nerve systems, as well as the control of chest wall movements during respiration by the cervical and thoracic spinal cord segments (Bosma

1986, 1992; Delaney & Arvedson 2008; Donner et al. 1985). Complex sensory feedback adjusts the swallow according to the size of the bolus, its homogeneity, viscosity, texture, moisture content, and taste (Barlow 2009).² By adulthood, control of the simple swallow will expand to involve 15–20 cortical areas, as well as the cerebellum – a rather astonishing fact given that simple swallow is an involuntary act (Hamdy et al. 1996; 1999; Mistry & Hamdy 2008; Mistry et al. 2006).

When we think of human development, we tend to regard birth as its single most important milestone. Yet as Prechtl (1974) had emphasized, the very fact that birth is abrupt ensures that birth – a momentous event for all concerned – cannot be, primarily, a developmental milestone for the infant.³ Instead, birth is the human infant's least forgiving hard deadline. The price of failure is suffocation, starvation, and/or infection through aspiration. A recent study on breastfeeding in Ghana illustrates this point (Edmond et al. 2006). Under “natural” conditions (i.e., without modern medical intervention) healthy, full-term newborns who fail to breastfeed within 24 hours after birth were 2.5 times more likely to die as infants. The study estimated that 16% of infant deaths could be prevented if newborns suckled within the first day; fully 22% more newborns would survive if feeding began within the first *hour* after birth. Given the costs, aerodigestion must be “good to go” well in advance of the blessed event.

The mechanics of suckling turn out to be surprisingly complex. At a first guess, new parents might expect suckling to be like drinking through a straw: Suck inwards and the milk will soon follow. However, neonates do not inhale through their mouths. They are nose-breathers unless under duress. Instead, infants extract milk by a combination of positive mechanical pressure and negative air pressure, both caused by tongue and jaw movements (Bosma et al. 1990; Crompton & Owerkowicz 2004; Thexton et al. 2007). Suckling begins with the “acquisition” phase: The infant's tongue protrudes and curls under the breast, then retracts to pull the breast into the mouth. At the same time, the infant's lips close tightly over the aureole, forming a seal; the sides of the tongue curve up and around the breast while pressing the breast and nipple tightly against the palate. The infant is now ready to express the milk. Once more, the tongue is the central player. Imagine attaching a wet suction cup to the bottom of a glass shelf. As the cup is flattened, it adheres to the shelf and forms a tight seal. To break that seal, a sharp tug is required. In suckling, the tongue acts like a travelling suction cup. As the infant's jaw opens, the tongue's seal to the breast is broken. This unleashes a peristaltic wave that travels down the length of the tongue, expressing the milk by positive mechanical pressure. The milk then flows into a “bowl,” created by a concave area at the back of the tongue. When enough milk has accumulated, this pooling initiates a simple or pharyngeal swallow.

In sum, suckling – a capacity of critical importance to infant survival – is a highly complex motor sequence in which the tongue plays the starring role. Suckling requires fine-grained motor control of the tongue (e.g., for changes in the shape and rigidity of the tongue), precise sequencing (e.g., for peristaltic motion of the tongue), and coordination of a diverse group of muscles (e.g., of the lips, tongue, and jaw). Importantly, suckling is a *sensorimotor* task, not a motor task alone. No infant comes into the world “wired

for” a breast of a certain shape, size, and rigidity; a specific brand of baby bottle; or milk of a certain viscosity and rate of flow. As we will see, virtually all of the task parameters are variables in suckling, the values of which change in real time as the infant suckles (German et al. 2004). This makes suckling the first and arguably most complex task controlled by a sensorimotor system in the human body.

In the next section, we outline a theory of human aerodigestive development. At present, we know more about the aerodigestive development of human infants than of any other species. Much of this research comes from medical research on premature infants, mostly through video, imaging, or post-mortem studies. But for obvious reasons, invasive physiological experiments are not performed on human newborns. Therefore, inevitably our theory relies on mammalian research more generally, from which we can extrapolate to the human case based upon shared mammalian traits such as tongue musculature, sub-cortical/cortical motor control, and basic sequence/rate of neurodevelopmental events.

4. The behavioural development of aerodigestion

4.1. Pre-natal aerodigestive development

The physiological complexity of suckling and swallowing – and the necessity of its tight coupling with respiration – explains why aerodigestive development begins well before birth.

Movement in the human fetus begins at about 7 weeks of gestation with strange lateral side bends of the head or the rump that occur at 1-second intervals (Lüchinger et al. 2008). These are notable in that they are the only fetal movements that are truly “stereotyped”: Repetitions of side bends do not vary in frequency, force, timing, or exact patterning. Between 7 and 8.5 weeks, the arms and legs start to make small, slow, single-direction movements that last a few seconds. A period of transition begins at 9 weeks: “General movements” or full-body movements involving the head, neck, trunk, and limbs appear. Gradually, over the next 4 weeks, general movements replace the more primitive side bends. By the 32nd week of gestation, the human fetus's postnatal motor repertoire is complete (Kurjak et al. 2004; Miller 2003; Yigiter & Kavak 2006). In the last 8 weeks of pregnancy, the fetus increases dramatically in size and weight yet the frequency of all movement decreases markedly.

Ultrasound observation of the human fetus suggests that the first feeding behaviour – a rudimentary swallow – begins at approximately 9–10 weeks gestational age (GA) (de Vries et al. 1982; Miller 2003). This is the same week in which the human fetus starts to make isolated arm and leg movements and to hiccup. This first swallow usually occurs prior to basic head movement (turning side-to-side, anteflexion, and retroflexion), breathing movements of the chest, and hand-to-face movements, all of which emerge one week later. Suckling begins gradually as a set of rudimentary behaviors, the “proto-components” of the mature suckling sequence. The first tongue movement, at 15 weeks GA, is a forward, rigid thrust of the tongue to edge of the lips – “tongue thrust” – that corresponds to the movement that presses the breast against the hard palate. The second tongue movement to emerge is “cupping,” the formation of the tongue into a bowl-like

shape, similar to the movement which catches and collects the bolus before swallow. Tongue cupping becomes a consistent motion at about 28 weeks GA. Finally, anterior-posterior motion – tongue protrusion and retraction of the kind tested by Meltzoff and Moore – is seen at 18 weeks GA. *This back-and-forth movement, out of and back into the mouth, is a precursor to the one that draws the breast into the mouth. In utero, it can be elicited by orofacial contact, by the fetus's thumb in the mouth, her cheek*

brushing against the umbilical cord, and so on (Miller 2003). Like cupping, TP/R is well defined by 28 weeks GA and occurs in combination with tongue-cupping and tongue-thrust (Fig. 2). Importantly, the same range of orofacial behaviors observed by ultrasound at 32 weeks of gestation will be present after birth. Indeed, within the first 15 minutes after birth, 95 % of all full-term newborns make spontaneous TPs, almost all of which occur within the first 3 minutes (Hentschel et al. 2007). An early study by

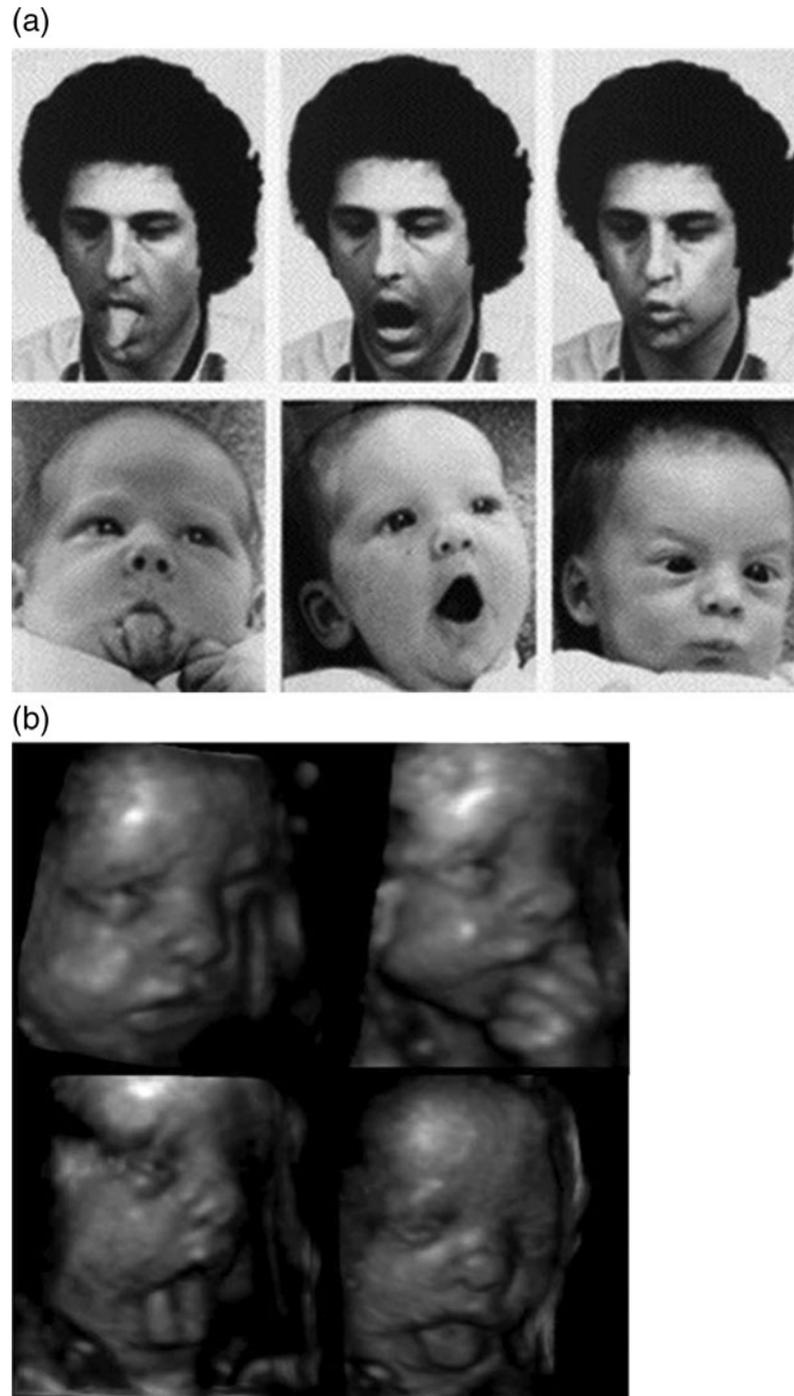


Figure 2. (a) Orofacial gestures of the experimenter and the neonate (Meltzoff & Moore 1977). (b) Four orofacial gestures of a fetus at approximately 28 weeks gestational age. (Top left) grimacing; (top right) finger sucking; (bottom left) tongue protrusion to the side; (bottom right) tongue thrust. (Kurjak et al. 2004).

Heimann et al. (1989) recorded the baseline rates of TP at days 2 or 3 after birth, at age 3 weeks, and finally at age 3 months. At 2–3 days after birth, 59 TPs were produced (32 weak, 27 unequivocal). At age 3 weeks, this figure dropped to 18 “medium-to-strong” TPs and by age 3 months, only 4 spontaneous TP’s were produced, a significant drop in incidence. These results were corroborated by Piek and Carman (1994). Small, large, straightforward TP/R motions along the median and lateral TP/Rs are all seen *in utero* and immediately after birth.

Gradually, the repetitive, simple behaviors of early gestation are integrated into smooth motor sequences. At 15 weeks GA, amniotic fluid is drawn into the mouth by inhalation-like movements of the chest. Sometimes the lips of the human fetus close after the bolus enters, sometimes not. At this stage of development, the bolus is drawn into the oral cavity without prior TP/R; occasionally tongue “fluttering” occurs prior to inhalation. By 28 weeks GA, however, once the individual components of suckling are refined, the bolus is drawn into the mouth by TP/R and then is held by the cupped and elevated rear portion of the tongue. Often the soft palate makes contact with the back of the tongue, securing the bolus in the mouth before the simple swallow. At this point, fetal swallowing differs from the adult version. In the human fetus, the bolus is propelled down the pharynx by a single large muscle contraction as opposed to the smooth peristaltic (wave-like) motion in the adult. Moreover, the opening at the fetal nasopharynx is left open during the swallow and the amniotic fluid flows freely into the nasal cavities. Similarly, the glottal folds that protect the lungs from aspiration in the adult are often open during swallow at 28 weeks GA. In other words, the adult mechanisms that guard the nasal cavities and the lungs do not function in the human fetus. Finally, during the fetal swallow, the epiglottis protrudes into the pharyngeal tube but it does not stand upright or make contact with the soft palate, as it will in the neonate. Swallowing in the fetus differs substantially from that of the adult, as well as from neonatal swallowing.

In short, the development of aerodigestion occurs through constant prenatal “practice.” The lips and jaws open and close as do the aerodigestive valves; the tongue protrudes and retracts; the chest expands and contracts, and the moving waves of contraction that define peristalsis flow down the length of tongue, the pharynx, and the esophagus. Through rhythmic repetition, the proto-components of aerodigestive behaviours emerge and transform into primitive motor sequences that then evolve into smooth, tightly coupled motor runs. In other words, rhythmic behaviour seems to be an essential part of aerodigestive development for both the acquisition of repetitive movements and their coordination by sensorimotor controllers. Tongue protrusion and retraction is just one element of this gestational process.

4.2. Postnatal development

At birth, the respiratory and digestive systems are unevenly matched in maturity. Respiration is immediately robust and reliable (Greer et al. 2006) whereas digestion can mature only given the complex stimuli of actual breastfeeding – the warmth, viscosity, and taste of milk, the smell, texture, variable shape, and “solidity” of the breast, and so on. At birth, the human infant has a simple suck-

swallow pattern: one swallow follows one suck. Over the first month, the infant learns to contain and corral milk within the mouth, to produce greater pressure with the tongue, and to increase the rate of peristaltic tongue motion. By the end of the first month, the suckling sequence is now organized into runs of several sucks followed by one swallow. Suckling efficiency measured by the volume of milk per suck and per swallow almost doubles. By 6 months, mature suckling is characterized by faster and more rhythmic suckling, longer suckling bursts, larger volumes per suck, and greater integration and stability in the suck-swallow rhythms (Gewolb & Vice 2006; Mizuno & Ueda 2001; Qureshi et al. 2002).

This maturation of the suckling requires the parallel evolution of a system that switches control between respiration and digestion (Amaizu et al. 2008; Qureshi et al. 2002). In adults, approximately 75–95% of swallows begin during the expiratory phase of respiration, a pattern that gives the adult some measure of safety. If the glottis or the nasal passages are left open during the swallow, there is still enough air in the lungs to expel the fluid with a short, sharp exhalation (not unlike how a whale clears its blowhole on surfacing). For the neonate who swallows up to 60 times per minute during suckling and yet who still lacks the precise motor skills of the adult, this adult pattern is too risky. At 48 hours after birth, when only colostrum is excreted, the adult pattern is dominant. But by the end of the first week, newborns shift towards swallowing *after* inhalation but *before* exhalation begins (Kelly et al. 2007). This is safer because the lungs are fully inflated just before the swallow. By 6 months of age, this pattern remains predominant. It continues until after the infant’s first birthday – that is, through the risky period during which infants learn to ingest solid foods (Gewolb & Vice 2006; Lau et al. 2003; Mizuno & Ueda 2001).

4.3. Defining the first period of aerodigestion: Safeguards during learning

In the months after birth, then, the sensorimotor control of aerodigestion matures by repetition. Of course, improvement by practice presupposes error, and, during this first year, there are a number of protective mechanisms in place (Reix et al. 2007; Thach 2001; 2007). One safeguard mentioned above is the neonatal pattern of respiration. Predominantly nose-breathing also markedly reduces the risk of fluid aspiration. However, between 6 and 12 weeks after birth nose-breathing ends, just around the time when the mother’s immune system no longer protects the infant from colds, and so forth. (Note to new parents: Even a neonate can “override” nose-breathing during nasal congestion [Rodenstein et al. 1985] through crying.)

The laryngeal chemical reflex (LCR), a set of chemoreflexes, is another safety mechanism. *In utero*, the glottal folds open to regulate lung pressure by releasing acidic lung fluid into the larynx (a necessary part of developing lung capacity). In response, the chemoreceptors inhibit breathing and stimulate the swallowing of amniotic fluid to reduce acidity in the larynx. After birth, the LCR functions as a protective mechanism against acid reflux. And later in life, the LCR will transform again, now into a protective mechanism that stimulates cough. (Unfortunately, the same protective mechanisms that work so well in the

full-term neonate works against the pre-term infant. Reflux can trigger life-threatening periods of apnea and bradycardia in these infants [Miller 2002; Praud & Reix 2005; St-Hilaire et al. 2007; Thach 2010; 2007].)

A final protective mechanism, the position and function of the neonate epiglottis, is relevant to our thesis. Infant aerodigestive anatomy and physiology differs from that of adults. In the adult, the upper and lower respiratory tracts are displaced, connected by a short length of pharynx. During the adult nutritive swallow, when the bolus nears the opening to the larynx, the epiglottis—the flap-like structure attached just above the glottis—folds down over this opening.⁴ Solid food or liquid passes over the tip of the flattened epiglottis on the way to the esophagus. For many years it was assumed that the epiglottis seals the glottis, thereby protecting the adult from fluid/solid aspiration. (Indeed, almost any text on aerodigestive physiology will contain this “fact.”) However, the epiglottis does not form a watertight seal over the glottis (Bosma et al. 1990), and so cannot prevent liquid from entering the lungs. The key to epiglottal function lies with the neonate. During the mammalian neonatal period, the openings to the upper and lower respiratory tracts sit directly across from each other. (Recall that the epiglottis is a purely mammalian organ.) In this configuration, the epiglottis sits high in the nasopharynx under the nasal cavities. During swallow, the epiglottis stands upright with its tip touching the uvula. Milk flows down the pharynx, around the base of the upright epiglottis, in two deep rivulets on either side of the open glottis (Pracy 1983). The upright epiglottis thus maintains a patent airway between upper and lower respiratory tract such that, in principle, the neonate could both suckle and swallow at the same time. However, in practice the epiglottis acts only as a safeguard. German et al. (2009) have shown that, in the newborn pig, the vocal folds close during nutritive swallow; they close the airway. Thus, as the neonate learns to integrate the copious new sensory cues of suckling after birth, the upright epiglottis serves as a safeguard against mistakes. This finding meshes nicely with Miller’s

(2003) observation that, even at 28 weeks GA, the nasopharynx remains open during swallow, but the glottal folds occasionally open and close.

Note that all of the aforementioned protective mechanisms bracket a period of aerodigestive learning that coincides with the period of TP/R “imitation” (Fig. 3). Nose breathing ends between 6 and 12 weeks after birth, just after the phase during which respiration and suckling are coordinated. The combined reflexes of the LCR start *in utero* to wash away acidic lung fluid during breath holding (closure of the glottis). They continue through the second month of postnatal life as a means to clear the esophagus of reflux and prevent reflux aspiration. Between 2 and 4 months, when the infant becomes susceptible to respiratory viruses, the LCR produces cough to clear the respiratory tract. In other words, the LCR matures in lockstep with changes in the aerodigestive system, first by producing apnea and swallowing in the perinatal stage, and then by initiating cough prior to the onset of respiratory infections and ingestion of solid food. Lastly, the epiglottis maintains a patent airway until respiration and suckling are fully coordinated—that is, just before “training” for mastication begins.

4.4. Switching to solids: Why tongue protrusion ends

The preparation for the mastication and ingestion of solid food (and the production of speech sounds) begins to occur around 3–4 months of age. This transformation, from suckling “machine” to self-feeding infant, requires both anatomical and physiological changes (Fig. 4).

The most critical anatomical event, the descent of the neonatal hyoid bone and larynx, consists of two components, a horizontal component that lowers the hyoid relative to the palate and a vertical shift that lowers the larynx relative to the hyoid (Lieberman 1968, 1975, 1987; Lieberman et al. 2001; Nishimura 2003; Nishimura et al. 2006; Sasaki et al. 1977). Descended larynges are now documented in several mammals, including deer, gazelles,

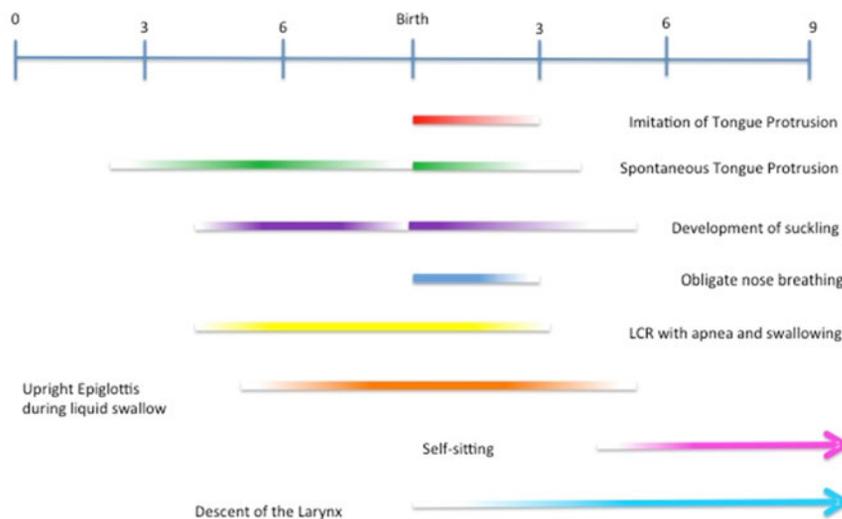


Figure 3. This developmental timeline shows the onset and time period of a number of aerodigestive events in human development. Note the coincident timelines of the imitation of tongue protrusion with the end of the first phase of human aerodigestive development: the mastery of suckling, swallowing, and respiration.

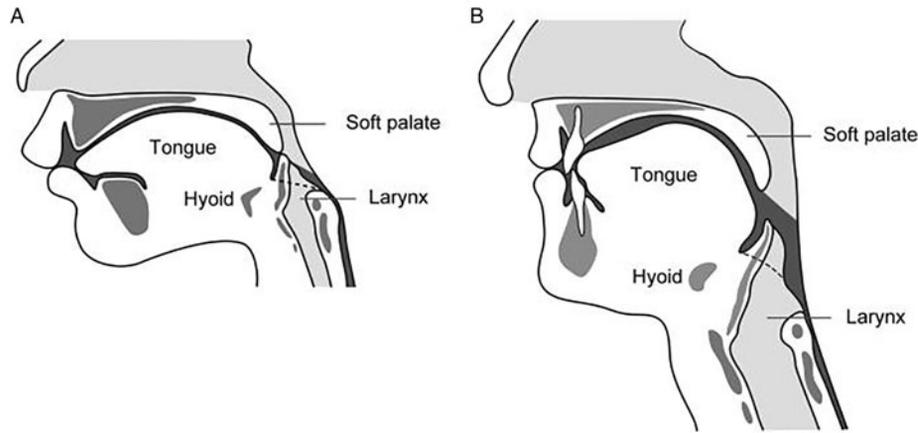


Figure 4. Anatomical differences between the adult and neonate aerodigestive systems. In the adult, note the position of the epiglottis, which sits well below the soft palate. In the infant, the soft palate and epiglottis touch. Note also the differences in the tongue shape and positions: The neonate has an elongated tongue with a flat surface; it sits forward, with the tip of the tongue just over the gums. In the adult, there is empty space within the oral cavity to allow tongue movement. Tongue movement in the neonate is more restricted (Matsuo & Palmer 2008).

lions, jaguars, tigers, cheetahs, and domestic cats (Fitch & Reby 2001; Frey & Riede 2003; Weissengruber et al. 2002), but in primates, the developmental pattern is only documented in chimpanzees so far (Nishimura 2003; Nishimura et al. 2006). In human infants, this descent begins slowly after birth; by 4 months, the infant pharynx contains the short connecting portion between the upper and lower aerodigestive tracts. As a consequence, the glottis is repositioned well below the openings to the nasal cavities. The epiglottis no longer makes contact with the hard palate during swallow, nor does it stand upright to maintain a patent airway. The resting position of the tongue is also shifted, from just behind the gums towards the back of the oral cavity. This new posterior position of the tongue makes it possible for infants to adopt the adult swallow. To swallow solid food, the tongue pushes the bolus into the pharynx and blocks the entrance to the oral cavity with its posterior end (in order to prevent the return of the bolus). When a liquid bolus is swallowed, the tongue participates in blocking the nasal cavities (to prevent aspiration). This shift in tongue position is accompanied by a newly rounded hard palate and the dissolution of the neonatal cheek fat pads. Together, they create room for new kinds of tongue movement—side to side, up and down, and back and forth—all within the oral cavity. With these changes, the tongue is ready to collect, masticate, and maneuver food, as well as practice speech sounds.

Unfortunately, this freedom of movement carries a cost. For one, the epiglottis, now positioned further down the pharynx, can no longer act as a safeguard against an ill-timed glottal closure. Consequently, the coordination of glottal closure with swallow must be mature by this stage. Second, the new posterior position of the tongue makes it possible for the tongue to inadvertently stop respiration during sleep. This problem is solved by a new form of tongue control, a brainstem mechanism in the hypoglossal nucleus (HGN) that coordinates inhalation with rhythmic TP/R. With each exhalation, the HGN is disinhibited, an event which causes both a slight TP/R and an increase in the rigidity of the pharynx, both of which create a patent airway (Bailey et al. 2006; Fregosi 2008; Fuller et al. 1999; John et al. 2005; Richardson & Bailey 2010).⁵

The second change in tongue control is more obvious. The infant must acquire the ability to manoeuvre food during mastication and prior to swallowing. Infants begin mouthing behaviour (touching an object to the lips or putting it into the mouth so that it touches the tongue and gums) at about 2–3 months of age. Mouthing increases over the next few months and peaks at around 6–9 months (Rochat 1989). This time period coincides with a critical period for learning to manipulate food of diverse textures; it also coincides with the most dangerous period of food-related asphyxiation in infants. Foods that break into hard pieces produce the most trouble: Nuts, carrots, apples, and candy are the main causes of asphyxiation (Altmann & Ozanne-Smith 1997). Mouthing wanes by 9 to 15 months once infants are well versed in eating solid foods (Fagan & Iverson 2007). These data suggest *that infants do not “explore the world by mouth” so much as explore their mouths with the world.* The infant develops a sensorimotor oral topography by using whatever objects are close to hand and hands are, literally, always within reach. Large objects that vary in shape, size, texture, taste, thermal conductivity, and rigidity make ideal sensory substitutes for the variety of foods that will soon be chewed and ingested—or at least for any neurologically sound infant with healthy gag and cough reflexes.

The development of mastication begins around 4 months of age, when the infant can sit upright for several moments without assistance. In the coming weeks, self-sitting will be the cornerstone for a variety of goal-directed behaviors—target-directed head and eye movements (Goodkin 1980) and reaching-to-grasp (without being pulled over by the weight of the extended arm). Self-sitting also indicates sufficient cortical control to sustain the grasping, mastication, and deglutition of solid food, the result of the myelination of the corticobulbar and corticospinal tracts. This correlation is not a coincidence. The safest position for the ingestion of solid foods is upright, not supine (Sears et al. 1990). A bolus of solid food requires greater mechanical and air pressure for smooth movement along the aerodigestive tract. As a result, the effects of gravity are integrated, through learning, into adult deglutition as a part of normal function: Remove the effects of gravity, and

swallowing becomes disorganized and unreliable even when the “solid” food is only a masticated marshmallow. The advent of cortical control also explains another sign of readiness to feed: the extinction or inhibition of the primitive reflexes. An infant who reacts with tongue thrust to every foreign/novel substance is not ready to taste and swallow new foods. Infants can transition safely to solid food, then, only when the cortical control of the sub-cortical pattern generators of respiration, suckling, and swallowing is in place.

To summarize, the first phase of human aerodigestion stretches from the 9th or 10th weeks of gestation to approximately 3 and 4 months after birth – from the onset of the first isolated aerodigestive movements to the mastery of suckling and the flawless coordination of swallowing with respiration. Throughout this learning period, numerous safeguards forestall potentially fatal accidents. Once mastery is reached, the second phase of aerodigestion begins, again prior to the onset of the new aerodigestive function: here, the ability to eat solid foods. During this period of transition, the tongue is repositioned to the back of the oral cavity, the palate gradually assumes a bell shape, and the fat pads disappear. All of these events allow the tongue to move freely within the oral cavity, to manipulate, masticate, and form a solid bolus. Importantly, these new aerodigestive tasks require flexible and novel tongue movements, including the ability to find, flip, and re-position solid foods onto the molars and point-to-point ballistic movements that require topographic information (i.e., from point A to point B). Cortical control is a necessary part of learning how to eat and, later, how to speak. And because of this, aerodigestive midbrain mechanisms, including TP/R, must be suppressed. Thus, TP/R ends when cortical control begins.

5. Spontaneous tongue protrusion as rhythmic stereotypy

In 1979, Thelen published a landmark, longitudinal study of the “rhythmic stereotypies” (or general movements) of infants. Twenty infants were filmed every 2 weeks, from 4 weeks after birth to age 52 weeks. Over one year, she recorded more than 16,000 instances of repetitive stereotypical body movements classified into 47 different kinds, among them hitting, kicking, banging, thumping, and flapping. She found, first, that the peak, postnatal frequency of each stereotypy was determined by anatomy – for example, all stereotypies involving the leg such as kicking with alternate legs, or synchronous heel-thumping peak at 20 weeks postpartum. Second, 84% of the stereotypies recorded (~16,000 events) had identifiable releasers such as the appearance of the caregiver, presentation of a toy, or an interruption to feeding. Yet these stimuli were remarkably nonspecific and unrelated to the rhythmic behaviors elicited. “It is as if the eliciting context demands of the infant, ‘Do something!’ – Greet the caregiver, express delight in the mobile, manipulate the toy – but the immature central nervous system (CNS) responds in a manner that is not goal directed” (Thelen 1981b, p. 240).

Thelen did not record the facial expressions of the infants studied (for methodological reasons) nor did she have access to high-resolution 4-D ultrasound images of pre-natal behaviours (including images of internal rhythmic

motor events). Had she, it would have been evident that although all infant stereotypies develop prior to birth, after birth they divide into two rough groups based on the timing of peak frequency. Aerodigestive stereotypies peak in frequency at birth whereas general stereotypies of the head, trunk, and limbs (that Thelen herself studied) peak months later. (The single exceptions to this division are finger movements, present at a low frequency from birth onwards.) One physiological explanation for this difference is simply that, in mammals, the myogenesis and synaptogenesis of the tongue and pharynx occurs much earlier than the development of the limbs and trunk, and even the jaw (Widmer et al. 2007; Yamane 2005). Another such explanation is that the corticobulbar tract, which mediates the cortical control of the trigeminal, facial, and hypoglossal cranial nerves, develops both earlier and faster than the corticospinal tract that controls limb movement (Martin 2005; Sarnat 2003). But as to why this should be, our answer at the outset seems the most plausible: Aerodigestive sensorimotor development takes precedence over the acquisition of “non-essential” general motor tasks at least until the second stage of aerodigestive development when trunk control is acquired and solid feeding can begin.

The experimental results of Thelen (1979) combined with the early ultrasound studies of neonatal neurologists (de Vries et al. 1982; Prechtl 1985) show that infant stereotypies form a class on the basis of seven factors as follows. Stereotypies (1) are simple, rhythmic movements; (2) begin and end within a set window during the first year of the infant’s life; (3) are invoked or undergo a change in rate as a result of nonspecific stimuli often related to arousal; and (4) re-emerge in later life as a result of cortical injury or generalized cortical degeneration. When an infant fails to exhibit a stereotypy or the stereotypy shows a markedly abnormal pattern, it is often the case that (5) there is a cortical abnormality or injury in the infant; and (6) this abnormality will lead to a cascade of further developmental problems. Finally, (7) stereotypies are easily distinguished from primitive reflexes that occur as a result of specific stimuli and promote infant survival.

TP/R, as our model gesture, clearly meets these criteria. First, TP/R is a rhythmic behaviour, one rarely seen in full-term infants after the fourth month of life. Abnormal or continued TP/R beyond the neonatal period is often the result of developmental abnormalities. For example, children and adults with Down syndrome continue to exhibit spontaneous TP/R, often into adulthood. The problem here is hypotonicity, a lack of muscle tone in the tongue, lips, and jaw (Limbrock et al. 1991). Without proper internal control, the tongue flattens, assuming a broad, flaccid shape, and as a result, the tongue does not exert normal pressure on the hard palette during suckling. Without suckling pressure, the high arched shape of hard palate fails to change into the broad, rounded shape conducive to solid feeding (Mizuno & Ueda 2001). In turn, the jaw (masseter) muscles develop abnormally, and the misalignment of the jaw results in a cross- or overbite (Faulks et al. 2008; Shapiro et al. 1967; Thompson 1976). Eventually this hypotonicity will affect speech and even the child’s ability to make emotional facial expressions (Limbrock et al. 1991).

TP/R often reappears later in life as a result of degenerative cortical disease or cortical trauma. Dystonic TP/R occurs with advanced cortical degeneration, as a result of

Alzheimer's disease, pantothenate kinase-associated neurodegeneration (PKAN), and a variety of other genetic degenerative cortical diseases (Schneider et al. 2006). Involuntary TP/R, in the form of tongue thrust, in these cases may be life threatening: that is, severe enough to impair swallowing and breathing. And people who have suffered severe neural trauma, *even those who have an absence of all cortical activity* as measured by electroencephalogram (EEG), may also show spontaneous TP/R (Go et al. 2008).

TP/R is affected by arousal. In Jones (2006a; 2006b), infants who listened to the overture to *The Barber of Seville*, music chosen for its abrupt changes of pace and volume, showed a consistent increase in TP/R. Similarly, Jones (1996) found that infants responded with TP/R to flashing colored lights and dangling toys. Both stimuli were as effective at increasing the rate of (full) TP/Rs as the demonstration of TP/R. In response to this evidence, Nagy et al. (2013) have argued that increases in TP/Rs do not correlate with the standard measures of general arousal. But as Jones (2009) pointed out, at least within a certain range of arbitrary stimuli, infants respond with specific reactions, an increase in orofacial stereotypies overall but an increase in tongue protrusion in particular. Moreover, if heart rate is monitored, imitation of TP is preceded by significant heart rate acceleration, an independent and objective confirmation of at least one arousal response (Nagy & Molnar 2004). In short, the infant reacts with tongue protrusion to any interesting or arousing stimulus. (In sect. 7, we will return to this issue.)

Importantly, TP/R differs from what have been called the "primitive reflexes" of the neonate, with which it has often been confused. The primitive reflexes such as the rooting, suckling, and the Babinski and Moro reflexes are complex, automatic behaviors evoked by specific triggering stimuli (e.g., stroking the cheek, drawing a pencil along the sole of the foot, briefly – and safely – dropping the infant). Although some primitive reflexes are rhythmic (stepping and sucking), others involve a single motor sequence (e.g., the Moro reflex). They develop around week 25 of gestation, and although they generally disappear within the first year of life, it is not uncommon to see certain primitive reflexes in healthy, young adults (Brown et al. 1998). In contrast, TP/R develops earlier in gestation, does not have a single trigger, and is fully absent in healthy adults. However, both TP/R and the primitive reflexes can reappear after neural loss in cortex, as the result of normal aging or with degenerative neural disease (Bakchine et al. 1989; Burns et al. 1991; Damasceno et al. 2005; van Boxtel et al. 2006; Vreeling et al. 1995). Therefore, both neonatal stereotypies and primitive reflexes appear to be sub-cortical motor functions but of two distinct kinds.

In sum, TP/R fits the profile of rhythmic neurodevelopmental behaviour. It emerges as a result of subcortical function *in utero*, is inhibited and/or integrated with the advent of cortical control, is sensitive to nonspecific external stimuli, and often reappears in cases of cortical trauma or degenerative disease. Abnormal neonatal tongue protrusion can also lead to a cascade of developmental disorders. Of course, if TP/R is just one of many rhythmic stereotypies, this would explain why stimuli such as the overture to *The Barber of Seville* produce an increase in neonatal TP/R. It would also explain the phenomenon of TP/R decline: We no longer see TP/R

"imitation" after 3 months because rhythmic movements, as a developmental phase, come to an end as a whole.

6. Tongue protrusion and activity-dependent development

6.1. The general phenomenon: Activity-dependent development

In the previous section, we argued that TP/R is a stereotypy, one of the many rhythmic movements that appear before and after birth, which are neither goal-oriented nor triggered by specific stimuli. Yet despite their apparent "aimlessness," the ubiquity of stereotypies in mammalian development suggests that they constitute a functional stage in sensorimotor development (Thelen 1979; 1981b). Thelen hypothesized that rhythmic stereotypies "bridge the gap" between disorganized and goal-directed behaviours, that they form a "substrate" for the directed behaviours to follow. Recent work on activity-dependent development suggests an answer that aligns with Thelen's view: Rhythmic movements, such as TP/R, drive a series of activity-dependent neurodevelopmental events.

Pioneered by the classic work of Hubel and Wiesel (Hubel & Wiesel 1970; Hubel et al. 1977; Wiesel & Hubel 1963; 1965) on mammalian visual cortex development, abundant evidence now strongly suggests that neural activity modulates the development of the central nervous system (see Ben-Ari 2001; Blankenship & Feller 2009; O'Donovan 1999 for reviews). Once neurons are born, spontaneous, isolated activity begins in individual cells, which is characterized by a slow depolarization crested by a burst of activity. Soon this random activity coalesces into the synchronous activation of neighboring cells, with waves of activation flowing outwards from the locus. Notably, spontaneous activation is not confined to one area of the developing brain, say to motor or sensory areas alone. It has been recorded in the spine (Borodinsky et al. 2004; Hanson & Landmesser 2003; 2004; Whelan et al. 2000), as well as in the cerebellum, retina (Meister et al. 1991; Sretavan & Shatz 1986; Sretavan et al. 1988; Torborg & Feller 2005; Wong et al. 1993), cochlea (Tritsch et al. 2007), hippocampus (Garaschuk et al. 1998), and visual cortex (Siegel et al. 2012). Immature neurons throughout the brain—even neural progenitor cells yet to migrate to their permanent locations—are capable of spontaneous activation and signal propagation.

Spontaneous activity of the kind just described drives early developmental processes both directly and through epigenetic mechanisms. In Ca²⁺ spontaneous activation, for example, a Ca²⁺ transient leads to an influx of Ca²⁺ ions, an event that initiates further production of Ca²⁺ and amplifies calcium concentration within the cell (Gu et al. 1994; Rosenberg & Spitzer 2011; Spitzer et al. 1994). This sudden depolarization can initiate changes in the cytoskeleton, such as the growth of dendritic trees (Konur & Ghosh 2005) or the emergence of synapses. Additionally, this intracellular Ca²⁺ can lead to the expression of genes for cell development. For example, calcium transients can inhibit or excite DNA synthesis and thus, control the rate of cell birth or neurogenesis (cf. Fiszman et al. 1999; LoTurco et al. 1995); they can determine whether largely inhibitory or excitatory transmitters are produced (Borodinsky et al. 2004; Spitzer & Borodinsky

2008; Spitzer et al. 2004), and; they contribute to pathfinding during cell migration (Hanson et al. 2008; Kita et al. 2015) often in conjunction with chemical cues (Imai & Sakano 2011).

Importantly, what happens downstream, the effects of activity on cell maturation, depends upon a number of factors. One factor is the distance over which activation spreads, that is, only within the neuron, to near neighbors only, or to distal projections. A second factor is the activation “signature,” the unique variation on the burst-silence pattern produced (Kirkby et al. 2013; Spitzer et al. 2004). Shorten the inter-burst interval or alter the burst pattern and normal development will not occur. Finally, the causal effects of spontaneous activation are *state dependent*—that is, dependent upon previous activity and its effects on gene expression.

The upshot of this body of research is that activity dependence is a general developmental phenomenon. On one end of the continuum, sensory experience acts through the standard mechanisms of sensory transduction and transmission, and properties of stimuli affect neural organization. At the other end, neural organization arises out of variations in the standard pattern of long silences punctuated by short bursts of activity. But there are also a number of “in between” variations. Spontaneous activation can spread to mature neurons, thus propagating the signal to distal locations. Indeed, Khazipov et al. (2004) reported that visual signals, produced through photoreceptor transduction and transmission via retinal ganglion cells can lead to waves of spontaneous activity at the axon terminus, in the lateral geniculate nucleus (LGN), prior to maturation. Finally, activity-dependent development can be driven by self-induced sensory feedback. Spontaneous activity in motoneurons, within the spine, midbrain, or cortical motor areas produces muscle twitches. In turn, muscle twitches activate stretch and load receptors in the muscles, sensory feedback that initiates activity-dependent changes in sensory areas (Colonnese & Khazipov 2010; Khazipov et al. 2004). So, the self-production of sensory signals, caused by motor events with the classic burst-silence pattern, is yet another variant of activity-dependent development.

On the picture of development now emerging, neural development uses a rich form of neural scaffolding. Spontaneous activity can create temporary pathways between two regions and then eliminate or alter them once the scaffolding is no longer needed—for example, once a direct link between the two termini has formed (Khalilov et al. 2015; Luhmann et al. 2014; Shatz et al. 1988). Epigenetic processes can lead to neurotransmitter specification and then their re-specification at a later time (Spitzer 2012; Spitzer & Borodinsky 2008; Spitzer et al. 2004). Similarly, an existent excitatory neurotransmitter may become inhibitory (or vice versa) as a result of the activity-dependent expression of different membrane channel receptors (Blankenship & Feller 2009; Ford & Feller 2012; Wolfram & Baines 2013). Thus, the “storyline” of neural development looks much less like a pure cascade of events, each stage building on the last, and more like an economical solution to the Tower of Hanoi puzzle, a back and forth of developmental events that eventually results in the standard organizational patterns of the normal adult brain (Shatz 2012).

Against this general framework, the suggestion that rhythmic stereotypies participate in activity-dependent

processes is more plausible. First, if motor events can bring about neural development through self-induced, rhythmic activation, then TP/R, along with other rhythmic stereotypies, is a potential cause of activity-dependent development. For another, it is less mysterious why there is a mismatch between the time periods of human gestational events typically measured in days or weeks (or occasionally months) and the lengthy lifespan of rhythmic stereotypies (~9 months). If mammalian neural development adheres to a “use, dispose, and replace” principle, and/or to the dictum of “write rough and refine later,” then TP/R might well drive a sequence of distinct developmental events: for example, pathfinding from B to A, followed by pathfinding from B to C.

In what follows, we begin with a short section on the physiology of the tongue, a prerequisite to understanding the development of its control, and then outline three activity-dependent developmental events to which TP/R as a rhythmic neurodevelopmental behaviour plausibly contributes.

6.2. The neurophysiology of tongue control

The mammalian tongue has a remarkable structure: It is a tethered limb without an internal skeleton (Takemoto 2001). Without the constraints on motion imposed by a rigid skeleton and joints, tentacle-like limbs have an enormous range of deformation and (non-translational) motion, a bit like fiber optics compared to a flashlight. Tentacle-like limbs are also alarmingly strong (think of elephants and logs) yet capable of fast and accurate movement and deformation (Kier 2012). For example, during rapid speech, an adult speaker produces ~1,400 phonemes a minute, an extraordinary sensorimotor feat (Hiimeae & Palmer 2003).

The current, predominant theory of tongue physiology treats the human tongue as a solid muscular hydrostat, as a solid cylinder of muscle that maintains a constant volume under pressure, throughout deformation (Smith & Kier 1985; 1989; Takemoto 2001). Decrease its height, and the cylinder must widen; decrease the girth, and the cylinder must lengthen. This inverse relation is the central principle behind the human tongue’s physiology according to the hydrostatic theory. Because muscles contract on activation but are lengthened passively, all musculoskeletal systems involve muscle antagonists: When one contracts, the other lengthens and vice versa. Within a solid muscular hydrostatic, muscle antagonists are formed by their relative orientation. Muscles that run parallel to the tongue’s long axis shorten the tongue via contraction. Muscles perpendicular to the long axis—the vertical and horizontal transverse layers—narrow the tongue and thus, lengthen it.

In the human tongue, these principles are implemented by complex physiology: Eight pairs of muscles form concentric layers around the cylinder’s axis; each layer itself consists of finely interdigitated layers of muscle fiber (Takemoto 2001). The tongue’s core, for example, consists of three muscle groups each of which runs perpendicular to the axis, the transverse muscle interdigitated with the genioglossus and verticalis muscles. Thus, when the core contracts, the tongue narrows and protrudes. Importantly, deformation of the tongue always occurs under active resistance, by isotonic contraction (Pittman & Bailey 2009).

When the core muscles contract, the surrounding layer of parallel fibers provides active resistance to lengthening. Together, isotonic contraction plus muscle interdigitation add strength and rigidity to the tongue's structure and make complex deformation possible.

Not surprisingly (to motor physiologists at least), human tongue control is organized in the same way as limb control. At the level of the midbrain, tongue control is organized by activity, by the common repetitive behaviours in which the tongue plays a major role. At least five aerodigestive activities (respiration, suckling, swallowing, mastication, and licking) are controlled by central pattern generators (CPGs) located in the medulla and pons (Barlow & Estep 2006; Barlow et al. 2010; Dutschmann & Dick 2012; Smith et al. 2009). A CPG is any set of neurons that produces a pattern of activation and maintains a rhythm. So, by definition, even a pacemaker neuron, a solitary neuron that fires spontaneously at regular intervals, is a CPG. But in practice most CPGs are complex circuits of interneurons that produce rhythmic movement through reciprocal inhibitory and excitatory connections, some of which are regulated by pacemaker neurons and some not (Marder & Taylor 2011). On some definitions, CPGs are said to be circuits that can produce "fictive behavior," that is, can produce motor patterns without feedback or afferent signals. This is true: CPGs are capable of self-sustained behaviour. But again, *in situ*, the genius of a CPG is its ability to modulate rhythmic motor behaviour on the fly in response to signals from the senses, cortex, and from other CPGs (Harris-Warrick 2011; Marder 2012; Marder & Bucher 2001).

Aerodigestive CPGs are large-scale circuits organized in rough hierarchies, what one might think of as "CPGs within CPGs." CPGs for the simplest repetitive behaviours are recruited into larger networks that synchronize their activation into coherent motor runs. In turn, these circuits may themselves be recruited as the components of even larger CPGs. Aerodigestive CPGs are particularly complex given the functional overlap between aerodigestive behaviours, for example, suckling, respiration, emesis, and licking all involve TP/R. Barring the re-duplication of all low-level CPGs, there must be some means by which CPGs can be shared. In principle, there are a variety of forms that sharing could take, probably all of which are found in aerodigestive motor control. In the simplest case, large-scale CPGs with common components are loosely connected into a single network and "sharing" neural resources amounts simply to ceding control on the basis of competition or protocol (Gutierrez et al. 2013). A slightly more complex scenario involves a network of low-level components that can be activated in different orders, sometime using all of the components, sometimes not. In the most complex case, large-scale CPGs are genuinely multifunctional: A single pool of neurons collectively instantiates more than one CPG (Ramirez & Pearson 1988). Because neurons can express multiple types of synapses defined by the neurotransmitters they release (Briggman & Kristan 2008; Harris-Warrick & Marder 1991; Kvarta et al. 2012; Marder et al. 2014; Ramirez & Pearson 1988), functionally distinct neural circuits can exist within a single pool of interneurons. For example, the pre-Bötzing complex within the respiratory network can produce normal inspiration, gasping, or sighing (Doi &

Ramirez 2008; Lieske et al. 2000; Ruangkittisakul et al. 2008; Tryba et al. 2008).

At present, very little is known about the sensorimotor representation of the tongue in cortex (but see Laine et al. 2012; Sakamoto et al. 2010). What we do know is that there are topographic maps of the tongue and other oropharyngeal structures in S1 and M1 (Cerkevich et al. 2013; 2014) and that the large areas of the homunculi devoted to the tongue and other oropharyngeal structures, is explained by their fine-grained motor control and multiple sensory systems. As we will see, TP/R is likely to play a role in the functional development of S1 and M1, but it ends too soon to participate in the "wiring" of the many cortical areas involved in even the "simple" act of adult swallowing.

6.3. The emergence and refinement of tongue protrusion

Despite its paradoxical sound, we suggest that TP/R begins as an activity "for" tongue protrusion itself, that tongue protrusion begets tongue protrusion of a "more better" kind. By the time TP/R is clearly visible in the human fetus, at 14–16 weeks GA, the brain has undergone significant development. The sensory and motor cranial nuclei, including the hypoglossal nuclei, have been in place for more than 8 weeks (Müller & O'Rahilly 2011); all six layers of the cortex are almost completely formed (Clancy et al. 2000). Yet appearances aside, the visible structures/areas of the brain are not yet functional because they lack both the internal circuitry and distal connections to sensory transducers required for mature function. Significant development in the form of neural specification (and re-specification) must occur before birth and will continue thereafter.

Warp et al. (2012) presented the first fine-grained description of how spontaneous activation leads to permanent circuit formation in the swimming CPG in zebrafish. The side-to-side swimming motion of the fish is the result of a simple circuit. In each spinal segment, two pools of motoneurons innervate muscle around the spine, one for each side of the body. Within each pool the connections are mutually excitatory; across the midline, between the two pools, the connections are inhibitory. In swimming, a wave of activity flows down the spine causing ipsilateral contraction and contralateral suppression (inhibition of contraction). The development of the swimming CPG follows this same head-to-tail pattern. At the top of the spine, release of a Ca²⁺ transient within one motor pool of the first spinal segment causes sporadic random activity that soon coalesces into synchronous activity; synchronous activity soon spreads across the midline into the contralateral motor pool where isolated, random activation begins. Again, isolated activity coalesces and now spreads to the next spinal segment. At the same time, neural coupling matures: Activation by transient release leads to the formation of gap junctions, and activity across gap junctions results in the expression of synapses. Without spontaneous activity, or activity across gap junctions, further specification does not occur. This is how the swimming CPG is born of incremental, activity-dependent developmental processes (Warp et al. 2012).

As we have seen, prenatal ultrasounds provide behavioral evidence that aerodigestive brainstem CPGs also emerge in an incremental fashion: Mouth opening/closing, tongue

protrusion/retraction, and glottal opening/closing all begin with minute, uncertain movements that slowly develop into robust rhythmic motor sequences. We suggest that the CPG for TP/R develops along the same line. Motoneurons for tongue innervation that originate within the hypoglossus (cranial nerve XII) nucleus are grouped by muscle innervation (e.g., the genioglossus muscle) as well as by hydrostatic function. Two pools of motoneurons, in the medial and lateral branches of the hypoglossal nucleus, control tongue narrowing/elongation and tongue shortening/widening respectively (Guo et al. 1996; McClung & Goldberg 2000; 2002; Smith et al. 2005). We also know that in the early postnatal period (in rats), hypoglossal neurons switch from spontaneous/gap junction transmission to synaptic signaling. Thus, local spontaneous activation within the medial branch of cranial nerve XII explains the first weak protrusive movements of the tongue (by activation of the medial motoneurons). A widening circle of synchronous interneuron activation, representing muscle recruitment, explains the increasing strength of tongue protrusions. All else being equal, spontaneous activity in the lateral branches will cause tongue retraction. And like the neural pools on the opposite sides of the spinal segments in the zebrafish, inhibitory interconnections between the medial and lateral compartments ensures that, at the outset, tongue retraction does not hinder tongue protrusion and vice versa.

6.4. The interconnection and coordination of brainstem CPGs

Once lower-level motor components begin to emerge, they must be brought under the control of larger-scale aerodigestive CPGs. As we have seen, there are many ways that this can occur. Some neural circuits will be genuinely multifunctional: that is, capable of producing multiple distinct patterns like the pre-Bötzinger nucleus in respiration. Other CPGs might share a low-level circuit simply by passing its control back and forth between them, according to some engrained “rule” or on the basis of competition. But whichever strategies are implemented, both inhibitory and excitatory connections between the component CPGs are necessary: Inhibition ensures that mutually exclusive motor sequences are not activated by their shared components; excitation coordinates activation, binding motor components into synchronized sequences.

By the time TP/R is just discernible at 12 weeks post-conception in the human fetus, the sensory and motor nuclei of the cranial nerves have been in place for many weeks (Clancy et al. 2001). By the end of the embryonic period, at about 8 weeks post-conception (Müller & O’Rahilly 2011), all of the cranial nerves and nuclei have formed and occupy their permanent locations—even before the motoneurons have innervated tongue muscles. (The exceptions are the facial cranial nerves (VII) and their nuclei that form later in the early fetal period.) What remains is the development of functional circuits.

Consider two aerodigestive CPGs that share control of the tongue, the CPG that controls the oral stage of swallowing and the CPG that controls suckling. The oral stage of swallowing involves innervation of the mouth, face, tongue, palate, and pharynx (cranial nerves V, VII, IX, X, and XII). The larger CPG for suckling, which comprises at least six separate areas of the brainstem, involves the

(paired) cranial nerves V, VII, and XII (Broussard & Altschuler 2000). In feeding, suckling precedes swallowing—at first, in a cycle of one suckle and one swallow, but quickly progressing to one swallow after multiple suckles (sect. 4.2). Their coordination thus involves connections that suppress simultaneous activity yet allow each CPG to cede or gain control serially and allow flexibility, given maturational changes, of the suck-swallow rhythm. The control of TP/R involves the coordinated activation within the hypoglossal (XII), trigeminal (V), facial (VII), and glossopharyngeal (IX) cranial nerve nuclei. But TP/R also produces a cascade of sensory signals from the oral cavity, tongue, jaw, lips, and face, which will arrive simultaneously at the sensory portions of the trigeminal (V), facial (VII), and glossopharyngeal (IX) cranial nerves. Two of these cranial nuclei, V and VII, contain circuits common to both suckling and swallowing. So sensory feedback from TP/R will produce simultaneous activation in cranial sensory nuclei V and VII. (Cranial nerve XII, the hypoglossal nerve, is largely or entirely a motor nerve.) If neurons that fire together, wire together, then TP/R will produce interconnections between components of suckling and swallowing not initially connected—that is, between all those that involve the cranial motor nuclei V and VII. These are exactly the kinds of inhibitory connections needed to ensure flexibility in the suckling and swallowing sequence: No matter how many sucks precede the swallow, sensory feedback will inhibit the swallowing CPG.

In sum, robust TP/R can aid in the maturation of other aerodigestive CPGs because TP/R produces a wide range of—and widely ranging—sensory feedback to the cranial nuclei, relative to other oropharyngeal repetitive behaviours such as tongue peristalsis and glottal opening and closing. This goes some way to explaining why TP/R might continue to occur as an isolated behaviour.

6.5. The development of topographic maps in somatosensory cortex

In placental mammals, the formation of topographic maps within cortex, such as the motor and sensory homunculi, begins with the formation of a temporary developmental structure, the cortical subplate. Spontaneous activation within the subplate guides the axons of sensory neurons from the thalamus below, and the axons of cortical motor neurons above (Kanold & Luhmann 2010; Tolner et al. 2012). In mammalian development, the crucial anatomical structures that connect brainstem nuclei with orofacial somatosensory cortex—the cranial nuclei, the thalamus, the cortical subplate, and all six layers of cortex—form largely prior to the onset of TP/R (Clancy et al. 2001). Yet although TP/R begins too late to be a major determinant in the mechanisms of neurogenesis, migration, or axon pathfinding to S1, the development of functional circuitry in S1 has yet to occur.

During this postnatal period of mammalian cortical development, S1 has a single form of organized neural activity, spindle bursts, that correlate with motor activity: for example, muscle twitches in the hind limb of the rat produce temporally correlated S1 signals, and extinction of muscle twitches largely silences S1 (Khazipov et al. 2004). This suggests that spontaneous activity in M1 organizes sensorimotor cortical connections through self-initiated activity (muscle twitch). In much the same way that

postnatal visual experience is required for normal formation of the ocular dominance and orientation columns of mammalian V1 (for a review, see Cang & Feldheim 2013), sensory experience generated by self-motion organizes cortical homunculi. Thus, TP/R coincides with a period of dramatic cortical development driven by sensorimotor signals of the very kind required.

At this point, there is no direct evidence for the involvement of TP/R in these processes. This is not surprising: It is only within the past couple years that basic anatomical research on the cortical representation of orofacial regions (Cerkevich et al. 2013; 2014) has been completed. Still, TP/R and other orofacial behaviours continue into the postnatal period, and there is no lack of developmental events to which self-initiated signals might participate, namely (1) the generation of somatotopic S1 maps of the tongue, lips, jaw, and lower face; (2) the corticothalamic connections between facial/tongue regions of S1 and the ventral-posterior nucleus of thalamus (Deck et al. 2013); and/or (3) the corticobulbar connections between M1 and the hypoglossal, trigeminal, and facial nuclei (Sarnat 1989; 2003; 2015). These are all circuits/networks that we know form in the neonatal infant, for which tongue protrusion would provide the requisite “end point” of neural activity.

7. Rethinking neonatal imitation

Thus far we have walked through the events of the aerodigestive development and the essential role that sensorimotor control of the tongue plays within all aerodigestive functions of the human neonate. We hope to have established that TP/R (1) has the hallmark features of the rhythmic stereotypies common in early infant development; (2) emerges early in prenatal life and continues until suckling and respiration are fully coordinated and developed; (3) ends prior to the learning period, during which the infant prepares for the ingestion of solid food; (4) is controlled exclusively by brainstem mechanisms given the immaturity of sensory and motor cortex; and (5) likely contributes to at least three kinds of activity-dependent development during the lengthy window of its existence. Viewed in this context, the positive results of TP/R imitation are more likely to be by-products of normal aerodigestive development, behaviours that increase in frequency when neonates interact with adults or are presented with other interesting stimuli, than they are to be the result of facial imitation. The coincident window of appearance and disappearance of TP/R “imitation” with the first phase of aerodigestive development lends further support to the aerodigestive origin of TP/R (Fig. 3).

Starting at 12 weeks, the human fetus develops a repertoire of rhythmic behaviors, including TP/R, mouth opening and closing (MO/C), isolated eye opening (as opposed to repetitive blinking), index finger protrusion, mouthing (with hand in mouth), yawning, grimacing, smiling, and swallowing. As we have seen in section 4.1, all of these movements begin as small, isolated gestures and increase in duration and frequency over the following weeks. Eight weeks before birth the behavioral repertoire of the neonate is in place ready for postnatal life and all of the gestures tested in imitation experiments come from this repertoire. The aerodigestive stereotypies (plus

finger movements) peak in frequency at birth. Of these “early” stereotypies, TP/R and MO/C and index finger protrusion are produced with the highest frequencies during the first week after birth (Oostenbroek et al. 2016). It is worrisome that all of the stereotypies that peak early in frequency are also the gestures that are tested in neonatal imitation experiments. Are these gestures imitated because they are frequent gestures in neonatal life? Or do imitation experiments yield positive results *because* these stereotypies are more frequent?

The aerodigestive theory situates the gestures at issue within a known class of fetal/infant behaviours – stereotypies – but also within the known processes of early neural development. These stereotypies form a developmental stage in motor learning. This suggests a very different explanation of why the gestures used in neonatal imitation experiments peak at birth, taper off, and then disappear. Proponents often suggest that the infant has lost interest in old social interactions and has moved on to new, more novel behaviours. Instead, *all* early rhythmic movements end by this time. From the physiological point of view, then, orofacial stereotypies make sense as members of a well-defined category of fetal/neonatal behaviours. The same conclusion applies to the other stereotypies that appear to elicit imitation.

We realize most proponents of neonatal imitation will not be satisfied with this argument, especially those who do not support the strong representational claims of AIM. And even readers who accept our account of aerodigestive neurodevelopment may question the consequences of these facts for neonatal imitation. To conclude, then, we address three questions the proponent of neonatal imitation might reasonably ask.

7.1. Could there be a subcortical locus of NI?

Suppose we agree that neonatal imitation is unlikely to be controlled by cortical mechanisms and shift our focus to subcortical ones. Here the mammalian superior colliculus (SC) seems like the most plausible candidate. SC is a laminar, midbrain structure that uses visual and multimodal cells to perform sensorimotor transformations. Its structural and functional properties make it perfectly suited to neonatal imitation (cf. May 2006). Briefly, the superior three layers of SC (I-III) receive only visual input, from the retinal ganglion cells, V1, and the frontal eye fields (FEF). Superior SC conserves the topographic organization of the retina and V1, and its neurons preserve the properties of V1 cells (on-off center-surround organization, sensitivity to orientation and wavelength, and binocularity) (Tailby et al. 2012). The deep layers of SC receive input from multiple senses – vision, audition, proprioception, plus the somatosensory and vestibular systems – and they converge upon single cells in all possible combination (Sparks & Hartwich-Young 1989). These multimodal neurons are also topographically organized, forming three distinct maps, one each for visual, auditory, and somatosensory inputs, which align in location within and between layers (Meredith & Stein 1986b). The net result is a systematic multimodal mapping of neurons that “prefer” whatever stimuli are coincident in space and time (Meredith & Stein 1986b). The sight of a dog and the sound of its bark – in spatiotemporal synchrony – produce a maximal response in deep SC neurons. Finally, SC deep layers drive motor

behaviours: Efferent SC signals are sent to pre-motor and motor nuclei of the brainstem and spine (Meredith & Stein 1986a). All in all, the SC seems “purpose built” to implement the hardware for neonatal imitation.

7.1.1. Answer. Certainly, *prima facie*, SC looks like an excellent candidate. In fact, Pitti et al. (2013) have produced a model that shows how SC could transform visually encoded facial gestures into imitative actions using the receptive properties of SC neurons. This is not as surprising as it might seem. SC visual neurons and V1 neurons have very similar response properties with the possible exception of S cone input (but see Hall & Colby 2014). If we, as adults, recognize facial expressions/body gestures by means of V1 input, it would be very odd if one could not construct such a model from SC neural responses. Rather, the more significant question concerns the plausibility of the suggestion: Is SC likely to underwrite neonatal imitation?

Traditionally, we have understood the primary function of mammalian SC as one of orientation: In primates, the SC coordinates eye and head movements during saccades to maintain focus on visual targets (Marino et al. 2015; Schiller et al. 1987). It also controls smooth-pursuit eye movements when targets move slowly (Krauzlis et al. 2000), provides updates on current location (Dash et al. 2015), and activates express saccades. This orientation function is well preserved across mammalian species. It controls whole-body orientation away from threat in rats (Redgrave et al. 1996a; 1996b) and reaching behavior (towards a target) in cats (Courjon et al. 2004; Iwamoto & Sasaki 1990; Werner et al. 1997b), monkeys (Philipp & Hoffmann 2014; Stuphorn et al. 2000; Werner et al. 1997a; 1997b), and humans (Himmelbach et al. 2013; Linzenbold & Himmelbach 2012). More recent research suggests that SC also participates in target selection – in picking out an item of interest – whether or not orienting behaviour follows (Müller et al. 2005).

It is this feature of SC that is most relevant here. Insofar as infants orient towards adult faces in the first moments after birth, the SC is the most likely candidate for this orienting mechanism. For example, Johnson et al. (1991; 2015) champion a two-process theory of facial processing in which an innate sub-cortical system, called CONSPEC, biases orientation towards faces. This bias ensures salient input for the “training up” of cortical areas in facial recognition. Still, few researchers have held that the superior layers of SC themselves process for orofacial features and/or expressions. Rather, the question at issue is whether the SC visual layers are biased towards some feature that all and only faces have, or whether SC orients towards faces much of the time given general biases of SC I–III visual neurons at birth. Either way, SC is understood as a mechanism for selection and orientation, not for facial/gesture recognition. And recognition of different facial/bodily gestures is necessary for imitation.

Further, there is a more conclusive reason why SC could not be the basis of neonate imitation. Mammalian research suggests that the topographic maps of SC deep layers are formed and aligned by multi-stage developmental processes (see Cang & Feldheim [2013] for a review). *In utero*, chemical cues provide guidance for the axons of retinal cells into SC that preserve the topographic

maps of the retina and V1 (Triplett 2014; Triplett et al. 2012). Next, endogenous wave-like activity from the retina establishes connections that preserve topographic relations both within and between these layers (Furman et al. 2013). In the last stage, SC multimodal neurons undergo a critical period of plasticity, a learning period during which potentially multimodal cells adjust their response to reflect those modalities that prove most valuable (Balmer & Pallas 2015; Xu et al. 2014a; 2014b; 2015). Importantly, this critical period of postnatal plasticity cannot occur without input from association cortex (Jiang et al. 2001). So SC maturation requires (a) a functional association cortex, (b) functional connections between association cortex and SC, and (c) significant postnatal experience. In cats, this occurs 4 months after birth (Wallace & Stein 1997). Neil et al. (2006) estimated that human infants are 8 to 10 months old before this particular kind of multimodal integration is in place. SC is thus highly unlikely to instantiate neonate imitation because the crucial step of multimodal mapping does not occur in newborns.

7.2. Can there be imitation without representation?

Let’s agree for the sake of argument that neonates do not solve the correspondence problem through multi- or supramodal representations – or indeed through *any* representational system at all. Robust neonatal imitation could still occur. As the authors agree, infant stereotypies are produced through the coordinated activation of sub-cortical CPGs. Thus, the correspondence problem is more likely “solved” through resonance and entrainment. Think here of the aerodigestive system in the engineering terms of control systems. In a closed-loop system, sensory feedback produced during the last cycle of behaviour is used to approximate a set point of the system – that is, a value for one of the process variables – in the next oscillation. So in suckling, when the compression stroke of the jaw meets with resistance, the power stroke is adjusted to exert more force. Or in swallowing, feedback from the leading edge of esophageal peristalsis adjusts the speed/force of subsequent contractions. Yet because the “goal” of aerodigestive development is merely the smooth production of behavioural sequences often repeated thousands of times in an infant’s day, this network is unlikely to represent its process variables. Resonance and entrainment produce faster, more reliable results than could any feed-forward model of the process state. Of course, by adulthood even the sight of food on a plate will reset the parameters of swallow in anticipation (Leopold & Daniels 2009), presumably by means of the 15–20 cortical sites involved in producing adult swallow (Ertekin 2011; Ertekin & Aydogdu 2003; Sörös et al. 2008; 2009). But for the neonate, a continuous closed-loop control is a superior system. Thus, as long as the relevant visual stimuli release or entrain matching behaviour, the correspondence problem will be solved without representational matching.

7.2.1. Answer. Recent work on motor systems, including work on the mirror system, suggests that central pattern generators lie at the core of motor function in vertebrates (Grillner 2006; Grillner et al. 2005a; 2005b; 2008; Kozlov et al. 2009; Mahan & Georgopoulos 2013). Predictably,

many questions remain about how resonance might work for coupled oscillators *in situ*: How are sub-threshold activation patterns brought to threshold? What are the means of coupling? How are the values of the process variables modified? And how do cortical signals alter or entrain CPG motor outputs? These are all open questions, and we cannot insist that the resonance theorist answer them on demand. On the other hand, the biggest hurdle for anyone who champions a resonance theory of “matching” is the explanation of how the neonatal visual system encodes adult gestures that are registered/encoded by networks of oscillators. It is not enough to suggest here that seeing an instance of TP/R disinhibits the TP/R network or that recognition of an open mouth releases the CPG for MO/C. Mere association between a sensory input and a motor output is not imitation. Instead, there must be a systematic explanation of how the neonatal brain recognizes specific gestures and selects the relevant CPG by means of resonance. To solve the correspondence problem – to imitate – the infant must have a systematic means by which *this* arbitrary visual input is matched to *that* proprioceptive feedback, which is produced by *that* repetitive stereotypy, using the concepts of oscillators and control systems. This is a tall order.

We are not suggesting that the aerodigestive theory offers a better explanation of neonatal imitation, of course, because it is not a theory of imitation. But it meshes nicely with other areas of research that can explain what we observe in these experiments: that is, why infants orient towards the face of the model, watch intently as the model poses, and then produce general movements in response to that neutral face. Perhaps the infant orients towards the model’s face as a result of motion, novelty, or as a result of the orientation biases of visual cells in SC (Johnson et al. 1991; 2015). Although the gesture is demonstrated, a rudimentary form of turn-taking in the neonate suppresses general movements as a class (Dominguez et al. 2016). And when the model switches from TP/R to a neutral expression – or what amounts to a still face for the infant – the inhibition of aerodigestive CPGs ceases, and the most frequent stereotypies, as a function of age, are released. This is the kind of explanation that dovetails with models of early learning for gaze-following, emotional expression, facial recognition (of the mother’s face), and categorical perception (seeing faces as a special kind of object).

7.3. How to explain the neonatal imitation experimental data?

Let’s put aside questions of mechanism and talk about why neonatal imitation is a good explanation of the experimental results. Proponents of neonatal imitation have long argued that it fosters parental attachment, which is of vital importance to infant survival. As we come to know more about the social and cognitive development of infants, it seems clear that social interaction between the infant and caregiver is an essential factor in early motor, sensory, and cognitive development (Althaus & Plunkett 2015; Arditi et al. 2006; Ham & Tronick 2006; Lavelli & Fogel 2002; Messenger & Fogel 2007; Serrano et al. 1992). By itself, the aerodigestive theory does not explain the neonatal imitation

experimental data. It explains only why neonates would make aerodigestive behaviors.

7.3.1. Answer. Arousal theorists have often argued that the appearance of neonatal imitation is a general artifact of arousal (Anisfeld 1991; 1996; 2005; Jones 1996; 2006a; 2006b). Neonates orient towards salient visual properties and, once oriented, are aroused by this stimulation; once aroused, they increase the rate of some spontaneous movements. Human faces at close range – be it a face with a protruding tongue, or even a “still face” – are among these salient properties. We believe the arousal theorist must be right: We see increased orofacial stereotypies directly after birth and in the presence of other arousing stimuli such as human faces, music, moving inanimate objects, and so on. What the arousal theory has lacked, however, is an explanation of why neonatal arousal expresses itself in just this way, at precisely this time in development. Here we have the beginnings of an answer. At birth, the neurochemistry of the event creates unprecedented levels of arousal, which ensures a safe transition from an aquatic existence to land-based respiration and suckling (recall the survival value of suckling within the first hour after birth). This explains why the rate of orofacial “gestures” is greatest in the few moments after birth even without human interaction. When newly born infants are shown human faces, the visual biases inherent in (most likely) the superior layers of SC produce greater levels of transient arousal, which in turn causes ever more orofacial stereotypies. This same pattern of arousal and of transient orofacial gestures continues until the infant has mastered the mechanics of suckling and respiration – and until these rhythmic movements have produced the requisite changes in S1 and M1 functionality. In the weeks and months following birth, the infant broadens her typical response to arousal (Precht 1993). Orofacial behaviours fade as the other stereotypies (from among the 47 that Thelen observed) become dominant. Glee (or rage!) can now be expressed by more frequent “variations of kicking, rocking, waving, bouncing, scratching, banging, rubbing, thrusting, swaying, and twisting” (Thelen 1981b, p. 239). All of these stereotypies are likely to aid sensorimotor development of the spine, brainstem, and cortex. But in the grand scheme of human sensorimotor development, it is subcortical aerodigestion first, all of the rest sometime later.

We have not explained, so far, the differential responses of neonates to specific gestures: For example, why do neonates show more TP/R than MO/C after watching an adult model TP/R? One thing we can say, here, is that we know very little about arousal, and the development of arousal, in the neonate. One naïve tendency – to which both authors unwittingly succumbed – is to imagine that sleep/arousal patterns in adults are a good model for the infant. Because the fetus is clearly more active at certain times than at others *in utero*, we imagine that the fetus is therefore either asleep or awake, no matter how early in gestation. But as with most other systems in the neonate, the mechanisms underlying sleep/arousal are not yet mature (Nijhuis et al. 1982). Nor is arousal controlled by a single mechanism, an on-off toggle switch between sleep and wakefulness. Arousal is effected differentially by both exogenous stimuli and endogenous mechanisms (Wass & Smith 2014) and by interaction with both circadian and ultradian

cycles (Blum et al. 2014; Blumberg et al. 2014; Mohawk et al. 2012). In other words, we may now know, in the broadest strokes, why we should be dubious about the results of neonatal imitation experiments. But without understanding the mechanisms of infant arousal, how they develop, or the developmental relationships between attention, emotion, and arousal, we are definitely missing the fine brushstrokes required. Without this knowledge, it is impossible to control for confounding factors in neonate imitation experiments. Neonatal apparent alertness, fussiness, and crying—even vagal tone—are only gross measures of arousal, a central factor in NI experiments. So we know arousal is relevant to what we see in these experiments, but we do not yet understand how stimuli (such as TP/R, still face, the voice of the model, or the absence of the mother) affects, or fails to affect, more subtle measures of infant arousal. Is tongue protrusion more interesting than mouth opening? Is still face more unnerving to the neonate than an open mouth? Or is still face unnerving only when it follows a period of normal interaction? Presumably animal models will help us determine how social stimuli of particular kinds interact with the internal states of neonates, both mammalian and human.

We should also point out that despite the obvious plausibility of social explanations of neonate imitation, the evidence for the social hypothesis in this particular case is quite weak. There are any number of other mechanisms that promote human maternal/parental attachment that are simple and effective: skin-to-skin contact (Bigelow & Power 2012; Feldman & Eidelman 2003), breast-feeding (Kim et al. 2011), increased oxytocin levels during pregnancy and after birth (Feldman et al. 2007; Levine et al. 2007), olfactory cues (Fleming et al. 1999; Marlier et al. 1998; Schaal 2009; Varendi & Porter 2001), maternal voice (Ockelford et al. 1988), and the co-ordination of maternal-infant heart rhythms (Feldman et al. 2011). Most of these mechanisms are triggered in the course of normal infant care and can be explained in terms of regulatory/physiological mechanisms present at birth. Given the importance of attachment, it seems likely that further mechanisms of attachment will be discovered. The more known mechanisms of attachment we discover, however, the weaker the evolutionary argument that imitation is necessary for survival. In contrast, a competent neonatal aerodigestive system requires specific kinds of neonatal aerodigestive sequences, each comprising multiple stereotypes. Assuming that aerodigestive development occurs via activity-dependent processes, then, stereotypes such as TP/R and MO/C are a necessary part of human development.

8. Conclusion

In our view, a critical step in resolving questions about the development of complex psychological processes will be to examine them from different levels of explanation. The combination of advances in motor development and detailed neurophysiological studies of both humans and nonhuman animals could provide developmental psychology with a more biologically plausible view of infant development.

Understanding developmental processes requires going beyond the dichotomies of nature and nurture, innate

and acquired, and focusing instead on the broader biological principles that govern and constrain development. For example, developmental psychologists' interest in intermodal perception has generated a number of findings about the discrimination and cross-modal transfer abilities of young infants (Bahrick 1987; 1992; Bushnell 1982; Gibson & Spelke 1983; Gibson & Walker 1984; Lewkowicz 1986; 1992; Meltzoff & Borton 1979; Streri 1993; Streri & Molina 1994; Streri & Pêcheux 1986). However, this interest has not sparked any corresponding interest in either (a) the various contributions of prior prenatal and postnatal experience, (b) the various constraints arising from different developmental trajectories of sensory and motor systems, or (c) the specific processes and mechanisms whereby intermodal functioning is achieved and modified during early development (Bahrick & Lickliter 2000). Using different levels of analyses to fill the gaps between these kinds of developmental concerns could substantially inform the complex relationship between genetic, sensory, motor, and environmental influences on infant development.

What we have tried to demonstrate, in the preceding long story, is the interconnectedness of the mechanisms of the developing system. Suckling, swallowing, or indeed any behavior is not hardwired but rather is assembled in real time within a particular context as the product of multiple developing elements. Many factors routinely shape development, from the ordinary—such as the importance of suckling for survival—to the extraordinary—such as the size of the oral cavity and the forward position of the tongue. Developmental psychologists thus should take a broader perspective that acknowledges the complex and contingent nature of development and that seeks to integrate relevant data from developmental biology and neuroscience into a more coherent and comprehensive account of the ways infants develop. Such approaches have become increasingly prevalent in the study of motor development (Thelen et al. 2001; Thelen & Ulrich 1991), cognitive development (Bjorklund 1995; Richardson 1998), language development (Dent 1990; Zukow-Goldring 1997), personality and emotional development (Lerner 1988; Lewis & Granic 2002), and social development (Cairns et al. 1990; Fogel 1993), to cite but a few examples. This perspective has the potential to achieve a fuller and more useful understanding of development and could move developmental psychology away from extreme forms of nativism and towards a more integrated account of development.

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NOTES

1. Here, the term valve is used loosely. The set of mechanisms that seal each cavity is highly heterogeneous and dynamic, with a multitude of anatomical solutions to the problem of opening and closing, narrowing, and widening the various passages at issue (Fitch 2000; Hiemae et al. 2002; 1995).
2. If you despise green beans, boiled cabbage, or overcooked liver, you will not have trouble believing the above statement.
3. There are clear exceptions to this statement. For example, at birth, the respiratory motoneurons in the brainstem are suddenly disinhibited, allowing the infant to breathe. This would seem to be a clear maturational event.
4. The two known exceptions to the folding of the epiglottis during swallow are in the opossum and the toothed whale. The adult opossum swallows liquid around the standing epiglottis; the adult toothed whale can swallow meat without folding the epiglottis.
5. Recently, Lavezzi et al. (2010) have tied anomalies of the HGN to sudden infant death syndrome (SIDS)–death of an otherwise healthy infant during sleep for no discernible reason. The most frequent deficit of the HGN was hypoplasia (or the lack of development): in particular, the absence of interneurons responsible for the generation of inhibitory signals to the HGN motoneurons. In other words, during REM sleep, an immature HGN fails to properly innervate the tongue in coordination with respiration, and this in turn causes the loss of a patent airway – and for some reason, not yet known, a concomitant loss of arousal. This theory makes sense of the single factor that high-risk situations for SIDS (co-sleeping, prone position, fluffy blankets, etc.) have in common: namely, they are sleeping conditions that foster an increase in concentration of CO₂. This would explain why, just when the tongue assumes its adult posterior position and HGN must co-ordinate its signals with the respiratory phase, SIDS has its greatest incidence (Sasaki et al. 1977).

Open Peer Commentary

“It takes two to know one” – Tongue protrusion-retraction is only one small facet of early intersubjectivity

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Abstract: Tongue protrusion-retraction is critical to early nutrition but is also a gustatory-olfactory aspect of early infant social behaviour that is, in part, reliant on pre-natal exposure and learning. Most early development is necessarily dyadic and intrinsically associated with other aspects of social functioning.

It takes two to know one.

–Gregory Bateson, “Old Men Ought to be Explorers” (in Nachmanovitch 1982)

To be, or not to be, Ay there’s the point.

–William Shake-speare, *The Tragical Historie of Hamlet, Prince of Denmarke* (1603)

More detailed investigation of many phenomena in human behaviour often reveal a variety of mechanisms to be involved. This paper provides a helpful overview of the conflicting literature on

the neonatal imitation of tongue protrusion-retraction and a scholarly summary of much of the related neuroscience. With the focus primarily on oropharyngeal movements, I propose that the ontogeny of orofacial central pattern generators for suckling provides a sufficient explanation for this phenomenon. I take the view that the ontogeny provides a unitary explanation and support for the argument focussed on this small component of the repertoire of behaviours observed in caregiver-infant dyads.

Keven & Akins (K&A) state that “orofacial stereotypies are crucial to the maturation of aerodigestion in the neonatal period but also unlikely to co-occur with imitative behavior” (target article abstract). I accept that these movements are central to achieving the process of suckling and its nutritional end, but would suggest that because this is necessary, it is not necessarily a sufficient explanation. Their view reminded me of Polani and MacKeith’s statement that “The newborn infant may be described as a tonic animal with oropharyngeal automatisms and neurovegetative mechanisms” (Polani & MacKeith 1960).

The newborn infant is typically alert, interested, and socially responsive in the early hours after birth. Physically neotenus, and helpless without adult assistance to access nutrition, warmth, and care, engaging a responsive adult caregiver is critical to its survival. This physical helplessness is associated with a lengthier period of postnatal brain growth than is seen in any other primate (see Coqueugniot et al. 2004; de Graaf-Peters & Hadders-Algra 2006), with rapid apoptosis and fine-tuning of the systems required for survival based on experience.

K&A state, moreover, that “If NI [neonatal imitation] promotes infant survival we should see the same behaviours in other nonhuman primates with similar social structure, state of maturation at birth, and communicative gestures” (sect. 2, para. 5). I would accept that such evidence is limited. This evidence is limited in part, however, because of the unique extent of our postnatal brain growth, and in part because of the limitations possible on such extrapolations (Clancy et al. 2007).

Newborn infants have learnt to recognise their mothers (Hepper 2015). They recognise her vocal characteristics (timbre, prosody, pitch); the timing of her reactions to others; her movement patterns, breathing, and heartbeat (see Ullal-Gupta et al. 2013; Webb et al. 2015). Her amniotic fluid is recognised by smell (Schaal et al. 1998) as is her dietary intake (Schaal et al. 2000). Olfactory-gustatory processes are part of social responsivity. Birth itself contributes to the development of suckling (see Alberts & Ronca 2012). The infant’s behaviour and responsivity takes place within the context of a rich multisensory social environment and is effected by early experiences. I take issue with the view that developmental psychology accounts of imitation support an extreme form of nativism.

Rather than a crudely simplistic ethological model of specific characteristics as fixed factors eliciting parental responses, successful navigation of the process of early development requires a finely attuned reciprocal process of interaction that we have called *intersubjectivity* (see Feldman 2015; Trevarthen & Aitken 2001). Neonatal behaviour is not fixed but adjusts to elicit positive responses from carers (see Adamson et al. 1977). These factors are part of a complex pattern of interaction between infant and caregivers that evolves and is fine tuned by both caregiver and infant, enabling human survival.

A number of other behaviours seen in infancy have been subjected to similar scrutiny. Neonatal smiling, for example, was often discounted as “wind” and only interpreted as social by many researchers after the demonstration by Harriet Oster (1997) that social and nonsocial smiling could be clearly discriminated with the facial action coding system showing that, as well as getting wind, babies could really smile.

We are currently seeing the development of second-person neuroscience and the technologies to enable dyadic neuroimaging and explore the interactive basis to human communication (Grossman 2015; Schilbach 2015; Schilbach et al. 2013). This approach is

being applied to other poorly understood social situations such as autistic spectrum disorders (see Rolison et al. 2015).

The species *homo sapiens* is at the extreme on various evolutionary continua. Our neonatal ability to elicit care is highly developed. It seems to be the altricial state of our nonverbal communication that has enabled us to evolve so rapidly by ensuring that human infants have the capacity to both survive and to adapt to vastly different cultural and linguistic milieu.

Clearly, the phenomena which constitute neonatal imitation are overdetermined, and the aspects focused on by K&A do occur at an increased basal frequency in the early weeks as the infant develops the orofacial neuromuscular systems involved in feeding and coordinating this development with pandiculation. This increased early baseline prevalence is also true of the wider range of imitative behaviours (such as finger movements and lip pursing) seen in infancy and involved in many of the studies under discussion.

Confining the discussion to a frame of reference, in which an explanation is sought for tongue protrusion-retraction alone, is overly partisan and fails to embrace or account for the more general aspects of early behavioural synonymy. Although it fits within the authors' explanation of the development of orobucco-facial patterns involved in suckling, it fails to negate the parallel functions in interaction and the evolutionary survival pressures on development.

Changes to prevalence and capacity to perform different actions through early life, described in much of the Piagetian literature on development (Heimann & Plooj 2003) have failed to be appreciated in much of the literature on infant imitation (see, for example, Oostenbroek et al. 2016), and rarely adjust for background changes with age and development. I accept the point that Esther Thelen's meticulous work led to a revision in our understanding of stepping; however, I would suggest this has limited salience in discussing tongue protrusion.

Turning the tide: A plea for cognitively lean interpretations of infant behaviour

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Abstract: Keven & Akins (K&A) revisit the controversial subject of neonatal imitation through analysing the physiological foundations of neonatal spontaneous behaviour. Consequently, they regard imitative capacities in neonates as unlikely. We welcome this approach as an overdue encouragement to refuse cognitively rich interpretations as far as cognitively lean interpretations are conceivable, and apply this rationale to other phenomena in early childhood development.

During the past decades, research in developmental psychology came along with remarkable reports about the cognitive capabilities of very young children. Numerous studies seem to reveal that young infants master certain tasks targeting these capabilities at a far earlier age than previously assumed. The results are readily interpreted in the same way as with older children: that is, in terms of early or even innate cognitive competence. We will henceforth call them cognitively rich interpretations. In contrast, cognitively lean interpretations of the same findings—that is,

interpretations in terms of basic psychological or even physiological principles—attract much less attention, if uttered at all.

Newborns' apparent imitation of others' facial and manual gestures (Meltzoff & Moore 1977) has been a prime example for this trend. On the one hand, it has been interpreted as a process of active matching between others' and one's own actions (Meltzoff & Moore 1977), a primitive form of self-consciousness (Gallagher 2000), and even as the early basis of intersubjectivity, communication, and social cognition (Meltzoff & Moore 1999a). During the past 20 years, these cognitively rich interpretations have attracted much interest, despite a substantial number of failed attempts in replicating the original effects (e.g., Anisfeld 1996; Koepke et al. 1983). On the other hand, cognitively lean re-interpretations of neonatal imitation—for instance, assuming simple attentional processes or experimental artifacts—were brought forward (e.g., Anisfeld 1991; Heyes & Watson 1981). They were, however, surprisingly rare and are only slowly being perceived by a broader audience (e.g., Oostenbroek et al. 2013). To our mind, the work by K&A in analysing the physiological mechanisms of neonatal behaviour encourages a general debate about cognitively rich versus lean interpretations. It should be taken as a wake-up call for a stronger consideration of the cognitive and neurophysiological basics of infant behaviour, and it should foster re-interpretations of results for a wide variety of phenomena in early childhood development.

In this commentary, we present three further examples from the field of infants' perception of, and learning from, others' behaviour for which cognitively rich interpretations have been proposed, but for which cognitively lean ones exist as well: rational imitation, theory of mind, and natural pedagogy.

Gergely et al. (2002) reported selective imitation of new actions in 14-month-olds. Infants were more likely to imitate if the model performed the action deliberately than if the choice of the action could be justified by external constraints in the model's situation. The authors concluded that 14-month-olds are capable to assess the model's situation and her actions under rational aspects. This concept of "rational imitation" in infancy has henceforth received much notice and has provoked many follow-up studies which pick up the paradigm and the cognitively rich interpretation. Again, only few attempts have been made to find cognitively lean interpretations for this phenomenon (e.g., Paulus et al. 2011). Our own research showed that selective imitation might be simply elicited by attentional processes (Beisert et al. 2012). Infants who were habituated to the external constraints in the model's situation imitated just as often as infants in the situation without constraints. We concluded that infants in the original study were distracted by the unusual external constraints and simply did not focus their attention on the relevant aspects of the model's action.

Remarkable results about young infants' perception of others' actions have also been reported by Onishi and Baillargeon (2005). For instance, 15-month-olds looked longer if an agent searched for an object not at the place where she had actually placed it before, but at a place where the object, invisibly for the agent yet visibly for the infant, had just moved. According to the authors, 15-month-olds already understand that people may have false beliefs about reality and expect them to act according to these. The conclusion that infants acquire a theory of mind far earlier than previously assumed has attracted wide attention and motivated further studies along this line with still younger infants (e.g., Southgate & Vernetti 2014). On the contrary, Heyes (2014) presented a cognitively lean account for the results of this and similar experiments. She argued that the sequence of events which the infants witness comes along with changes of physical characteristics like colours, shapes, and movements in the test stimuli. Infants' perception might thus just be modulated by the level of novelty in the test stimuli compared to events encoded earlier in the sequence.

Finally, Csibra and Gergely (2009) proposed that infants are innately biased for learning from benevolent social interaction partners. According to Csibra and Gergely's natural pedagogy

theory, ostensive signals inform infants that they should be attentive and prepared for subsequent learning. *Ostensive signals* are social stimuli which directly address the infant. For instance, the authors showed that 6-month-olds follow the gaze of an adult only if it is preceded by ostensive signals like mutual eye contact or infant-directed speech, but not if it is preceded by nonsocial signals. Recent research, however, indicates that a more basal attentional account is sufficient to substitute this cognitively rich interpretation (Szufnarowska et al. 2014). Salient social stimuli – which were not directed at the infants and, therefore, had no ostensive character – enhanced gaze-following as well as ostensive stimuli. It thus seems that social stimuli, irrespective of whether they are directed at the infant or not, are per se attention-grabbing and thus enhance the infants’ alertness in the observation of subsequent actions.

A key principle in science is Ockham’s razor: in short, the selection of the simplest among multiple competing theories. As depicted by K&A, cognitively lean interpretations are not necessarily simpler than cognitively rich ones as regards the mechanisms they describe. Still, they are simpler as regards the background assumptions which are behind these mechanisms: basal psychological or physiological principles instead of the prerequisite of early or even innate cognitive competence. Roughly half a century after the cognitive revolution, we would like to argue towards turning the tide in developmental psychology and contemplating cognitively lean in place of cognitively rich interpretations of infant behaviour.

Multisensory control of ingestive movements and the myth of food addiction in obesity

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Abstract: Some individuals have a neurogenetic vulnerability to developing strong facilitation of ingestive movements by learned configurations of biosocial stimuli. Condemning food as addictive is mere polemic, ignoring the contextualised sensory control of the mastication of each mouthful. To beat obesity, the least fattening of widely recognised eating patterns needs to be measured and supported.

Keven & Akins (K&A) use recent evidence on the development of respiratory and ingestive movements to criticise claims that mimicry of tongue protrusion plays a role in attachment to carers. This commentary applies their criticisms to the notion that addiction to ingestion makes people unhealthily fat. Both sets of ideas are symptomatic of a syndrome of “multisensory neglect” in research. Ignorance of the configured biological and societal stimuli to each mouthful of food or drink largely accounts for the continued failure to reduce the contribution of excess energy intake to obesity and the resulting disease, disability, and distress.

Ingestion of mouthfuls is shaped and contextualised by diverse interactions among the external and internal senses (Booth 1985; Booth et al. 2011b). As K&A describe, using just the senses within the mouth, movements of the tongue rapidly become efficient at drawing the nipple along the upper lip to the hard palate. It should be noted that a few sessions of suckling are sufficient to change the full stretch of the tongue out of the mouth (K&A Fig. 2[a]) to a slight protrusion between the lips and side-to-side movements (Steiner et al. 2001). These sights of the tongue in the absence of the nipple show vacuum ingestive activity, anticipatory to the tactile context of the breast between the lips and the nipple protruding into the mouth. Without independent evidence from

emotional behaviour and autonomic physiology, there is no warrant for attributing sensual pleasure to the neonate from the taste of sugar on the tongue (Booth et al. 2010; Booth 2016).

K&A could have written more about the changing multisensory contexts of movement patterns as they mature. For example, in their opening paragraph, they imply that stepping disappears because of relative lack of leg muscle. The fuller account is that learned integration of gravity into the control of stepping central pattern generators (CPGs) can only begin when the legs are strong enough. To walk or run, the stepping CPGs have to be contextualised by learned coordination of proprioception with balance, touch, and sight. K&A recognise a supportive role for gravity in swallowing but could assert its necessity for locomotion.

In another of K&A’s examples, the infant’s orientation to a face, gaze is potently drawn and held by the iris, eyelashes, and eyebrow of each eye (sometimes plus spectacles!) by centre-surround connections in the retina and primary visual cortex (V1) on which all visual recognition depends. Talk of attractiveness, reward value, or pleasure in the eyes is otiose. We don’t accuse extreme extroverts of addiction to socialising.

Consumption of drinks and foods requires vastly more complex sensory control of the movements holding in the hands, sipping, biting, masticating, and swallowing. K&A cite re-setting of the swallowing CPG by the sight of food (Leopold & Daniels 2009). That word “food” hides the variety of shapes, sizes, and compressibilities of the solid and semi-solid items that the eater ingested previously, plus unique mixtures of soluble and volatile compounds (flavours), different temperatures, and haptic microstructures: that is, oral textures – both tactile (Booth 2005) and auditory (Mobini et al. 2011). When the infant begins to select mouthfuls, the hands, vocal tract, and whole body become coordinated with the jaw, lips, tongue, and pharynx following visual anticipation of the item’s multisensory identity. The appearance of an item of food is configured in memory with the levels of all its other distinguishing physical characteristics and cultural attributes (Booth & Freeman 1993; Booth et al. 2011b).

Therefore, an ingestive mechanism can be identified only when the social and physiological influences are specified. In research on ingestive behaviour, however, mere licking of the lips, curling of the tongue, amounts eaten, or ratings of eating are given empirically empty labels such as regulation, motivation, pleasure, hunger, and satiety, and are even assigned generic functions like reward, working memory, attention, and expectation. This systematic over-interpretation diverts thought and effort from measuring the multitude of highly specific interactions across and within sensory modalities that determine ingestion.

Investigators may implicate a sensory modality, and even a category of transduction (such as yellow color or sweet taste), but that is not enough, as K&A point out in conclusion. Action towards each sort of food or drink (or any other object) requires each afferent and efferent channel to be at a particular level of activity (e.g., Booth et al. 2011a). The information content which each channel transmits is combined into a limited number of types of quantitative comparison between present and past output-input relationships (Booth 2013a). Notional cognitive-affective functions dissolve into actual causal processes within the individual’s mind.

Until multisensory integration is specified, its neural basis must remain obscure. The medial edge of the subthalamic striatum, *Nucleus accumbens*, organises sequencing of ingestive movements via inhibitory interneurons on CPG systems. In the part involved in tongue protrusions, some cells are inhibited by tasting sucrose and excited by taste of quinine (Roitman et al. 2005). However, such isolated tastes, smells, and textures cannot elucidate the contextualised use of combinations of specific levels of gustatory, olfactory, tactile, auditory, and proprioceptive stimuli, let alone of equally crucial signals from the viscera and the visual field (Booth 2013b; 2015).

Parents’ various ratings of their infants’ eating measure a single trait of responsiveness to foods, which relates to at least one of the

many genes associated with obesity (Wardle & Carnell 2009). After the age of 30, dopaminergic hyperactivity is associated with higher body mass index (Dang et al. 2016). Dopaminergic synapses lower thresholds and raise gain in the striatum, increasing the precision of processing of sensory characteristics (Warren et al. 2016). That is, dopamine activity reflects responsiveness to food stimuli, as part of arousal, not the reward of learning (Benton & Young 2016; Kroemer & Small 2016).

To combat obesity, we need activities under multisensory control to be described in eaters' terms, not in terms only of nutrients (Booth et al. 2004; Booth & Laguna-Camacho 2015). Evidence on which sustained changes do most for keeping slim can then be collected and disseminated (Booth & Booth 2011).

Spontaneous communication and infant imitation

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Abstract: Infant behavior is viewed in a social-communicative context centered on the phenomenon of spontaneous communication. Symbolic communication is learned and culturally structured, intentional, consists of symbols, and is propositional in content. In contrast, spontaneous communication is innate in both its sending (display) and receiving (preattunement) aspects, non-intentional, consists of signs, and is non-propositional or emotional in content. It underlies infant imitation, interactional synchrony, primary intersubjectivity, emotional empathy, and mirror neurons; and it is associated with oxytocin.

Keven & Akins (K&A) argue that tongue protrusion and retraction (TP/R) are “orofacial stereotypies crucial to the maturation of aerodigestion in the neonatal period but also unlikely to co-occur with imitative behavior” (target article abstract). Although agreeing that their analysis of TP/R is valuable and helps to explain the phenomenon of imitation “drop out,” I do not agree with their conclusion that TP/R is unlikely to be an example of imitative behavior. K&A view infant behavior at the level of the individual. I present infant behavior in a broader, social and communicative context centered on the phenomenon of *spontaneous communication*.

Spontaneous communication has been defined to explain the expressive behavior of patients with *left and right hemisphere brain damage* (LHD, RHD; Buck & Duffy 1980). Patients were shown emotional images (e.g., of hospital personnel, landscapes, unpleasant scenes, unusual scenes) while being videotaped, and judges viewing them without audio guessed the category of image viewed on each trial. LHD patients, who cannot speak, showed strong expressive responses to the images: laughing and gesturing to images of favorite nurses, and in one case beginning to cry upon seeing an image of a starving child. RHD patients were expressive verbally—one saying in effect, “That is Nurse Jones, we love her, she is wonderful to us”—but in a monotone with no facial expression. LHD patients showed the most accurate nonverbal communication, in that judges could determine what sort of image they were viewing as well as or better than non-brain-damaged comparison patients. In contrast, RHD patients were significantly poorer in nonverbal communication accuracy, not different from Parkinson's patients in whom a lack of facial expression is a key symptom. The kinds of communication that RHD and LHD patients were using were fundamentally different: the communication of RHD patients is symbolic: learned and culturally structured, intentional, consisting of symbols, and propositional in content. In contrast, spontaneous communication

is innate in both its sending and receiving aspects, non-intentional, consisting of signs, and non-propositional or emotional in content (Buck 1984; 2014). A subsequent meta-analysis confirmed that LHD produces deficits in “nonverbal symbolic communication”—pantomime expression and recognition—as well as speech (Buck & Van Lear 2002).

Spontaneous communication sheds light on a number of controversies in the field, including but not restricted to infant imitation. Evidence of interpersonal synchrony was demonstrated in the 1970s (Condon 1982; Condon & Sander 1974). Trevarthen et al. suggested that mutually contingent responsiveness between mother and infant associated with such synchrony (e.g., mother and infant responding “online” to the flow of the behavior of the other) naturally affords *primary intersubjectivity*: infant and mother each automatically attune to the subjective state displayed by the other (Braten & Trevarthen 2007; Trevarthen 1979; Trevarthen & Aitken 2001). (Trevarthen is cited in the references but not the main text of K&A.) Frans de Waal (2007) viewed early spontaneous emotion communication systems to be the basis for more advanced cognitive empathy. His model suggests that advanced forms of empathy involving theory of mind and perspective-taking grow out of more elementary emotional empathy, both evolutionarily and developmentally, analogous to the levels of a Russian matryoshka doll. The ordinarily hidden inner pre-linguistic core of this process involves innate motivational and emotional potential to spontaneously communicate: to form strong attachments, including capacities for imitation and mutual contingent responsiveness (de Waal 2007). The development of cognitive empathy is seen to depend upon, and involve elaborations of, this hidden inner core of emotional empathy.

There is also evidence that mirror neurons afford the direct detection/pickup of the emotions of others via their displays, and many have suggested that mirror neurons are involved in emotional empathy (e.g., de Waal 2007; Decety & Jackson 2004; Keysers 2011). Indeed, the notion of spontaneous communication requires that innate displays be responded to automatically by co-evolved preattunements, and mirror neurons appear to fulfill that requirement nicely. Although the notion of mirror neurons in humans remains controversial (e.g., Heyes 2010; Hickok 2009), there is direct evidence of mirror neurons in human patients undergoing depth electrode study for epilepsy. Mukamel et al. (2010) found neurons in humans that acted like classic mirror neurons studied in animals, discharging during both the observation and execution of one specific action but not another. They also found “anti-mirror neurons” in the supplemental motor cortex that increased when a given action was performed but decreased when the same action was observed. Keysers et al. (2010) noted that anti-mirror neurons could disambiguate actions of self from the actions of others and selectively block automatic motor imitation.

Ruth Feldman suggested that there are three prototypes of attachment in human beings: parental, filial, and romantic love; and that these share common brain mechanisms underpinned by oxytocin (OT) in the promotion of trust, emotional empathy, and interpersonal synchrony. Intranasal OT increases synchrony between attached couples in double-blind studies. Interestingly, when a father received OT and played with his infant, OT increased in the infant (Feldman 2012). Although OT has been considered a “cuddle hormone,” its effects are not always positive. It may be better termed a (spontaneous) “communication hormone,” as its effects appear to increase communication, which in insecurely attached persons or vis-à-vis outgroup members may be negative (e.g., Shamay-Tsoory et al. 2009). Thus, neurochemical systems associated with OT may support parental caring, play, friendship, and romantic love; and at the same time they may foster xenophobia: the rejection and ostracism of those not deemed to be within the group.

Spontaneous communication is pervasive, ubiquitous, and omnipresent; and at the same time typically automatic, involuntary, and unconscious. It contributes to *syncretic cognition*: raw,

holistic, direct, immediate, and self-evident knowledge-by-acquaintance; whereas symbolic communication is associated with sequential, linear, propositional, and rational *analytic cognition* (Tucker 1981). From this point of view, infant imitation may be just another example of spontaneous communication. The infant's tendencies to exhibit TP/R, in addition to being involved in the maturation of aerodigestion, simply affords a way to display and communicate; and when TP/R ceases to occur, it outwardly appears to be "imitation drop out."

When dyadic interaction is the context: Mimicry behaviors on the origin of imitation

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Abstract: Keven & Akins (K&A) redefine some of the neonatal imitation (NI) behaviors as developmental stereotypes. From a neuroconstructivist framework, those early gestures are also far from being considered as imitative behaviors. The cognitive substrate of imitation requires an interactive context to develop. Prior to intentional imitation, the dyad shows *mimicry* behaviors, which are automatic, but do not fade through development.

Keven & Akins (K&A) re-analyze Meltzoff and Moore's (1977) results, re-interpreting the so-called NI of tongue protrusion and retraction (TP/R) gestures by the infant from an exhaustive description of motor control acquisition. They adopt a neurodevelopmental perspective that shares some crucial arguments with the neuroconstructivist model (Mareschal et al. 2007): developmental explanation; neural development as activity and context-dependent; multiplicity of contexts; chronotropy; lack of univocal correspondence between behaviors and cognitive processes; and interdependence among different levels (i.e., genetic, neural, cognitive, behavioral, environmental) both in psychological development and for the explanation of this development.

K&A's work constitutes a bright and parsimonious redefinition of TP/R gestures as developmental stereotypes (i.e., subcortically controlled, arousal dependent, and faded once infants acquire motor control), focusing their analysis on neural and behavioral levels. We strongly support the contention that NI behaviors neither fulfill the criteria for imitation nor that they are precursors for genuine imitation. The purpose of this commentary will be twofold: (a) to support this assumption from a cognitive level of analysis; and (b) to add some evidences emphasizing the relevance of dyadic interaction in the development of imitation.

Scientific evidence seems to show that the cognitive system of the newborn would not be prepared yet to accomplish all of the tasks involved in imitation. Their perceptive and attentional capacities (Volpe 2008), and face processing and intersensory processing abilities (Bahrick et al. 2004; Johnson et al. 2015; Lewkowicz 2014; Morton & Johnson 1991), among others, are too weak yet. In the following weeks, organism-environment interactions will shape the development of social orienting, and infants will soon be able to respond contingently to social stimuli. There is just a "chronotropic coincidence" between the progressive improvement in social orienting abilities and the fading of NI. We share K&A's disagreement with the social hypothesis view on the explanation of this drop-out "from a change in *performance* not competence, as the later emergence of sophisticated imitation makes clear" (sect. 2, para. 5). NI and

early social orienting abilities do not correspond respectively to a subcortical and cortical control of a unique behavior with the same cognitive and social function, but they follow distinct developmental lines. Imitation would be found only in the developmental trajectory of social orientation.

The beginning of imitation behaviors has been established by 6–8 months (Oostenbroek et al. 2016). However, in our view, there would be earlier specific types of behaviors, similar in their appearance to NI, but again with a totally different function and origin, that would be truly incipient forms of matching behaviors, and precursors of genuine intentional and intended (Carpenter & Tomasello 2005) imitation. Those were called *mimicry behaviors*, and have been scarcely considered in infants imitation studies (Moody & McIntosh 2006). Mimicry behaviors emerge in typical development when NI behaviors are disappearing, and while the infant is acquiring cortical motor control but before the development of cognitive functions involved in mature imitation. They are still automatic, non-intentional, and non-goal directed, but they imply the copy of a model and are triggered by a specific stimulus, not by general arousal. Even when involuntary, mimicry behaviors do also *form a substrate for the directed behaviors to follow*, and they have a clear social function (Carpenter et al. 2013; Moody & McIntosh 2006).

A clear example of those mimicry behaviors is social smiling. The social smile emerges around 8 weeks, coinciding with the 2-month shift: when infants show improved head control and gaze direction, increased alertness and sustained attention, and an increasing ability also to explore features of the face (Wörmann et al. 2012).

Consequently, significant changes in dyadic interaction between adult and infant arise during this second month (Lavelli & Fogel 2005). Another set of evidence shows that, when mother-infant dyads from two different contexts regarding the frequency of face-to-face interactions are compared, no differences are found at 6 weeks. However, at 12 weeks, the frequency of smiling behaviors is higher for the group of dyads in the more interactive context (Wörmann et al. 2012).

Thus, social interaction is needed for mimicry behaviors to develop, and they influence and are influenced by variables associated with social contact. Mimicry has been called the "social glue" (Lakin et al. 2003): It promotes affiliation, empathy, and pro-social behaviors, both in adults (Chartrand & Lakin 2013; Duffy & Chartrand 2015) and young children (Carpenter et al. 2013). In infant-adult dyads, from one side, mothers interpret an infant's imitation as an invitation to respond contingently (Wörmann et al. 2012). From the other, infants whose mothers show more imitative behaviors are more able to perceive contingency in interactions (Legerstee & Varghese 2001; Soussignan et al. 2006).

Interaction provides the dyad with *opportunities of repetition* (Thelen 1981b), and this repetition (with certain characteristics, not perfectly contingent ...) will progressively enable a mutual adjustment between infant and adult. From very early on, the presence and frequency of imitative behaviors is an indicator of positive interactions, regarding the sensitive responsiveness of the mother, the attentiveness to caregiver shown by the infant, and the degree of mutuality shared by the dyad (Wan et al. 2013).

Mimicry is a precursor of intentional imitation, but it does not fade when the dyad develops those more sophisticated forms of imitation. Some preliminary results from a longitudinal study we are carrying out on the developmental trajectory of imitation in infants show that mimicry behaviors increase in frequency from 9 to 15 months old. Mimicry behaviors would be acting as an enhancer of social interaction through development.

Earlier behaviors such as reflex smile or TP/R gestures are crucial in human development, and are part of an infant's repertoire of motor behaviors that will be used to imitate. However, our hypothesis, as is K&A's, would be that its function is far from sharing the developmental trajectory of imitation. Imitation

behaviors will develop in an interactive context, and mimicry will emerge in the beginning of that developmental trajectory, and will continue to promote interaction through its whole course.

The functional and developmental role of imitation in the (a)typical brain

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Abstract: Keven & Akins (K&A) propose a biologically plausible view of neonatal imitation based on the analysis of sensorimotor development. Here, we consider imitation in the general context of motor cognition, taking examples from both typical and atypical development. Specifically, we will discuss the functional role of imitation, its multi-level nature, and its anomalous features in autism.

The target article focuses on the phenomenology of neonatal imitation, a topic that has received considerable attention in the past decades. Its wide appeal results in part from the suggestion that neonatal imitation has a crucial role not only in the development of more complex imitative skills, but also as a building block of social cognition (Meltzoff & Decety 2003). This view would imply that humans—at least to some extent—are wired to imitate and socially interact. At the neural level, some theorists—as also reported by Keven & Akins (K&A)—implicate mirror mechanisms in neonatal imitation (Simpson et al. 2014a) and imitative phenomena in general (Iacoboni 2009b). As such, anomalies in brain mechanisms supporting imitation may trigger a cascade of effects on the acquisition of imitative and social skills, ultimately contributing to social interaction difficulties, such as those characterizing autism spectrum disorder (ASD; e.g., Casartelli & Molteni 2014; Kana et al. 2011). Although this perspective on the functional and developmental role of imitation has long been the mainstream view in developmental brain sciences, we posit, in line with K&A, that conceptual and experimental caveats continue to undermine the notion of imitation. For instance, the reliability of neonatal imitation in predicting future social skills is controversial, and recent longitudinal evidence even challenges the existence of neonatal imitation in humans (Oostenbroek et al. 2016; Simpson et al. 2016). Furthermore, following K&A's proposal, behaviors such as orofacial stereotypies are crucial to the maturation of the neonate's skillset, but they are not necessarily imitative instances. We may question whether the reasons that have sustained interest in the concept of imitation (i.e., its role as building block in social skills) would survive in the absence of a nativist model for neonatal imitation. Indeed, to consider neonatal imitation as innate is the classical way to bridge the gap between elementary and more complex (i.e., socially relevant) imitative phenomena. To contribute to this debate and, more generally, to understand the functional and developmental role of imitation in typical and atypical brain development, we stress the need to conceptually clarify the definition of imitation and reframe it in more operational terms. This may prove meaningful not only from a basic research perspective, but also from a clinical viewpoint. Below, we propose three initial considerations in this direction.

1. Separating origin and function of imitation. Since Meltzoff and Moore (1977) first uncovered the ability of newborns to imitate adults' facial gestures, the study of neonatal imitation

has aimed to define its contribution to the emergence of subsequent complex imitative and social skills. The questions of how and when the social value of imitation appears are surely interesting, but are secondary to understanding its *function*. Accordingly, we should not confound the origin and function of imitation. We claim that regardless of when the social properties of imitation emerge across maturation, and irrespective of their underlying mechanisms (e.g., genetics, learning, or both), the study of its features is crucial to describe (a)typical developmental trajectories. For example, this may help shed light on the pathophysiological mechanisms of ASD.

2. Imitation as a multi-level concept. We argue for an update to the concept of imitation into more basic components with distinct, although potentially interconnected, layers. This could reduce the ambiguities of experimental findings on imitation (for a similar debate on theory of mind, see Schaafsma et al. 2015). Addressing imitation as a multi-level construct will facilitate the identification (and empirical testing) of specific sub-processes, reflecting different degrees of abstraction. In line with studies on motor cognition focused on mirror-based motor action/intention understanding (for a review, see Rizzolatti & Sinigaglia 2010), we propose a similar conceptual framework for imitation. Thus, *to imitate* can refer to the imitation of proximal goal/motor act (e.g., to grasp an apple), or of distal goal/motor action (e.g., to grasp an apple to eat it). To imitate can also refer to the imitation of “motor prosody” or “motor style” (e.g., to grasp an apple to eat it *gently*; see also Casartelli & Molteni 2014). As long as we consider imitation as a monolithic process, these levels are neglected, and in turn, imitative phenomena (whether impaired or preserved) can potentially be misinterpreted. This is critical in the context of ASD in which misleading results or misinterpretations may bias clinical practice.

3. Imitative phenomena, motor interference, and ASD. Reformulating the concept of imitation as a multi-layer construct offers additional opportunities to evaluate markers that differentiate how neurotypical and ASD individuals encode (imitative) actions. Compelling studies describe how the social and nonsocial cues may affect motor output (e.g., during imitative tasks), raising alternative hypotheses on how social cues affect action production and/or action understanding mechanisms in ASD individuals. Thus, either ASD individuals do not attend to social cues that influence motor output, or they atypically select and/or process such cues. Studies on gaze processing and action in ASD individuals support a sort of immunity of the motor system to social cue interference (Becchio et al. 2007). However, studies on visuo-olfactomotor interference propend for atypical social cue interference. Indeed, children with ASD show preserved automatic imitation (namely, the kinematics of their movement are facilitated following the observation of a model performing the same action) only when action observation occurs in the presence of the maternal body odor (Parma et al. 2013). In other words, an olfactory social cue is able to kinematically perturb an imitative action (see the notion of “motor interference” in Casartelli et al. 2016) in an anomalous way with respect to neurotypical individuals. Systematically assessing if and how social stimuli interfere with imitation, and whether this is explained by mirror mechanisms, may be an effective way to characterize atypical developmental trajectories in ASD. The present commentary praises K&A's assessment of the development of imitation through a sensorimotor lens, and extends it with a perspective on how motor cognition may shape the concept of imitation. We propose a revision of the concept of imitation centered on its multi-layer nature. Besides revealing typical developmental trajectories, this approach represents an intriguing tool to study the pathophysiology of ASD with potential impacts on clinical practice (Ronconi et al. 2016).

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Does early motor development contribute to speech perception?

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Abstract: At the end of the target article, Keven & Akins (K&A) put forward a challenge to the developmental psychology community to consider the development of complex psychological processes—in particular, intermodal infant perception—across different levels of analysis. We take up that challenge and consider the possibility that early emerging stereotypes might help explain the foundations of the link between speech perception and speech production.

Following their detailed elucidation of early appearing stereotypes in tongue movements, Keven & Akins (K&A) challenged the developmental psychology community to reconsider other early appearing complex psychological processes, such as intermodal speech perception, from this perspective. In this commentary, we take up that challenge by considering the role of early motor development in speech perception. Specifically, we address the question of whether the steps in prenatal and early postnatal development in the infant's developing control over tongue movement could provide information about the size, shape, and movement capabilities of the oral articulatory apparatus, and whether this in turn could provide a mapping onto which both heard and seen speech can be projected. We use as reference previous work from our lab showing that temporarily impeding tongue movement interferes with consonant discrimination in young infants (Bruderer et al. 2015).

K&A provide persuasive argumentation that tongue protrusion and retraction (TP/R), and a host of other behaviours that are categorized as stereotypes, are functionally important for setting the foundation of the aerodigestive system. The stereotypes fall into a class of processes that is spontaneous and activity dependent. The result of these processes in development, they argue, is an initial organization of the somatosensory and motor cortices relevant for successful coordination and movements of oral-motor articulators involving the mouth and tongue, such as cupping, sucking, breathing, and swallowing. We put forward for consideration the hypothesis that these same TP/R and other related stereotypes may simultaneously provide the infant with a mapping of the shape and configurability of the (upper) vocal tract, and how that changes with movement of the articulators. This, in turn, although not necessarily essential for speech perception as it is for aerodigestion, may underlie the infant's integration of heard, seen, and self-produced oral-motor movements even before the onset of babbling.

There is experimental evidence of sensorimotor influences on speech perception in the first six months of life. As highlighted in the target article, infants as young as 4 months (Kuhl & Meltzoff 1982) and even 2 months (Patterson & Werker 2003) can match auditory and visual speech, looking longer to the face that matches the sound they are hearing. At 4 to 5 months of age, infants' auditory-visual matching of the vowels "oo" and "ee" is modified if infants purse their lips around a pacifier or their caregiver's finger (into an "oo" configuration) versus if the infants' lips are stretched by a teething toy or their caregiver's finger (into an "ee" configuration) (Yeung & Werker 2013).

It has also long been known that from birth infants can discriminate many non-native, and therefore unfamiliar speech sounds, and that an important part of speech perception development entails a decline in non-native discrimination by the end of the first year of life (see Werker & Hensch 2015). Recently, we found that at 6 months of age, impeding tongue movement can disrupt auditory discrimination of non-native consonants

(Bruderer et al. 2015). We tested infants' ability to discriminate the Hindi dental /d̪a/ versus retroflex /ɖa/ distinction, a non-native, and therefore unfamiliar distinction that English-learning infants can discriminate at 6 months of age. These consonants are produced by placing the tongue tip either against the back of the front teeth (dental /d̪/), or against the roof of the mouth (retroflex /ɖ/). We prevented tongue movements in the experimental condition by having caregivers hold a flat teether over their infants' tongues, and allowed tongue movements in the control condition by having caregivers hold a soft u-shaped teether against their infants' gums. Tongue-impeded infants failed to discriminate the non-native speech sound distinction, whereas tongue-unimpeded infants successfully discriminated the consonant contrast.

Neuroimaging studies using diffusion track imaging (DTI) in neonates show that the establishment of white matter fiber tract connections that characterize the language pathways in the adult brain has already begun *in utero* (Dubois et al. 2015; Leroy et al. 2011; Perani et al. 2011). Just 2 days after birth, newborn brains are marked by an established ventral pathway, which will later be responsible for sound-to-meaning mapping; a superior dorsal pathway, extending from the posterior superior temporal sulcus (pSTS) to the premotor areas; and a diminutive inferior dorsal pathway that connects the pSTS to Broca's area (Perani et al. 2011). These dorsal speech pathways underlie speech sound-to-motor processing (e.g., Poeppel 2012). Within the first few postnatal months, the maturation of the inferior dorsal pathway outpaces that of any other regions within the language network (Leroy et al. 2011). Indeed, motor areas in the inferior frontal cortex—those connected by the inferior dorsal pathway to the auditory cortex—are activated by 7 months of age when infants listen to speech (Kuhl et al. 2014). The presence of these dorsal pathways may be key to our reported behavioural results suggesting motor influences on auditory-visual (Yeung & Werker 2013) and auditory speech perception (Bruderer et al. 2015).

Prenatal preparation for speech is evident not only in DTI studies of language networks, but also in auditory specialization to both simple sounds and speech sounds by 28–32 weeks gestational age (wGA) as tested in preterm infants with electroencephalography (EEG) (Mahmoudzadeh et al. 2017). Orofacial movements *in utero*, including TP/R (which is well defined by 28 wGA), could help establish the link between the motor cortex and the auditory cortices. The reported existence of the early appearing dorsal pathway prior to birth (Perani et al. 2011), together with the rapid development of the inferior dorsal pathway in the months following birth (Leroy et al. 2011), provides a plausible means by which sound-to-motor mapping could be established prior to, or immediately upon first experience with, linguistic experiential input.

Stereotypes, including TP/R, may support the functional specialization of the speech pathways specifically dedicated to auditory-motor mapping. A key notion in the target article is that stereotypes, exemplified by TP/R, are activity-dependent processes that contribute to the organization of the somatotomy of the tongue and the lips, as well as the cortico-thalamic (Deck et al. 2013) and the corticobulbar connections (Sarnat 2003) (pp. 50). The onset of TP/R occurs too late in development to inform neural migration, neurogenesis, or axon pathfinding to S1, but the functional circuitry of S1 is only beginning to be established when these stereotypes first appear (pp. 49). Whereas prenatal structural connections of the linguistic pathways are largely genetically determined (Kolasinski et al. 2013), spontaneous activity-dependent processes may contribute to their functional connectivity and integration. Therefore, the dorsal speech pathways that are present at birth may have been organized in part by the stereotypes that first appear *in utero*.

In summary, as K&A suggest, "infants do not 'explore the world by mouth' so much as explore their mouths with the world" (sect. 4.4, para. 3). This experience-expectant process (Greenough 1986) through which self-produced stereotypes and externally

heard speech interact with emerging anatomical connections may be the means by which early links between perception and production – even prior to babbling – are established.

Beyond sensorimotor imitation in the neonate: Mentalization psychotherapy in adulthood

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Abstract: Despite the persuasiveness of Keven & Akins' (K&A) review, we argue that mentalization, or the ability to interpret the mental states of oneself and others, is required to construct the neonate mind, going far beyond sensorimotor imitation. This concept, informed by certain psychoanalytic and attachment theories, has produced a form of therapy called *mentalization-based psychotherapy*, which aims to improve emotional regulation. Our aim here is to shed light on a form of neonatal imitation that goes beyond sensorimotor imitation.

From birth, “instinctive” behaviors have a double explanation, partly attributable to heredity (genes) and partly to the environment: The innate potential to develop behaviors, and behavioral acquisition and development, respectively. Gene–environment interactions normally explain interindividual behavioral differences, according to human behavioral genetic research (McGue & Bouchard 1998).

Very early on, as in imprinting (Lorenz 1935), heredity and environment interact. Some interactions occur in periods considered critical, being of limited duration and essential for subsequent normal development – for example, of language and vision. Many cerebral structures have critical maturation periods, corresponding to critical development periods for cognitive or executive functions, which enable cerebral plasticity (Hensch 2016). Cerebral plasticity may be newly available by reactivating critical periods using pharmacology, exercise, or psychotherapy.

Mentalization-based therapy identifies precocious mentalization mechanisms in neonates and children and attempts to modulate them in adults through psychotherapeutic interactions (Deseilles et al. 2015).

The critical interactions between adults and neonates depend on the neonate's behavioral capacities for social interaction (Brazelton 1987). At birth, neonates turn their head towards a human voice, are attuned to the pitch of a female voice; prefer human to pure sounds; fixate on images of the human face; turn towards the smell of milk; and so on. The neonate already interacts as an individual. For Brazelton, parents should be aware of their newborn's awakenings and sensitivities. Recognizing the neonate's competencies allows obtaining a starting point for interaction and imitation, both sensorimotor and psychic.

The capacities described by Brazelton corroborate those that Bowlby (1978) described as attachment, reflecting the quality of relationships established with others from birth through childhood and even adulthood (Zelinka et al. 2014). A key concept here is the internal working model: Mentalizing includes the abilities (1) to interpret the other's psychological characteristics; (2) to infer and attribute to the other desires, emotions, beliefs, and intentions; and (3) to differentiate and understand these mental states in the other and oneself. Children apply these models to various situations in order to predict their own and others' behaviors. Bateman and Fonagy (2006) called this interpretive *mentalization*, or the *interpretive interpersonal function*, arising from interactions with attachment figures.

Bateman and Fonagy (2006) contended that, at birth, humans are unaware of the different emotional states, and that they

learn through interactions with others, chiefly primary caregivers. Emotional states are learned by “mirroring” bodily sensations associated with emotional states, which the caregiver provides, particularly through facial mimicry and emotional aspects of the voice (resonance). This forms the basis for emotional regulation (Deseilles et al. 2015, p. 203): “I don't know where Mommy is, which gives me a stomachache and makes me cry. I see my Mommy, with tears in her eyes, who tells me ‘Don't cry, Mommy's here! I deduce that what I feel is grief, and I label it as such.” When children have difficulty with emotional learning, they incorrectly attribute emotions to bodily signals and have difficulty regulating emotions as adults. Mirroring enables children to develop appropriate emotions and emotional interpretations as the caregiver shapes and gives meaning to their internal experience. This provides emotional representations that are internalized in the psychic functioning, and that form the bedrock of the child's identity, or self. Emotionally neglected children, such as borderline personalities, lack a stable structure of the self. For normal development, children need exposure to significant individuals whose emotions they can represent within themselves, and who, in a caring and benevolent manner, can reflect their feelings and intentions appropriately, without overexaggeration, which may lead to overidentification with the other.

Children who lack adequate caregivers have problems distinguishing reality from fantasy, or physical reality from psychic reality. Bateman and Fonagy (2006) called this the *alien self*, or confusion with the other: internally experienced ideas and feelings do not seem to belong to the self. The child may then integrate the part of the other that feels like a stranger.

If children fail to learn that internal experiences exist in the mind and not in the external world, they may believe that the internal and external world are one and the same, with no differentiation between the imaginary and the real. Physical reality becomes “too real.” Moreover, in pretend mode, the mental state is completely separate from the external world, and external physical reality becomes “too unreal.” Normally developing children integrate the two modes to develop reflective mentalization, whereby thoughts and emotions are experienced as symbolic representations, such as words. Internal and external reality are experienced as simultaneously related and separate, and no longer need to be even similar or dissociated from each other. However, patients with borderline disorder do not integrate the two aspects, by default, and they function either in psychic equivalence or pretend mode.

The aim of the mentalization-based therapeutic approach is to reinstate the mentalizing process. Therapists should continuously ask themselves why the patient is saying something. What is the reason for the behavior? Why does the therapist simultaneously feel what the patient feels? Therapists strive to understand what is disturbing their patients, how to identify and give meaning to their experience, and how to clarify it to them. Therapists must also accept enacting the transference experience, evoking the alien self. Therapy takes place in the here and now, not the past or future. Therapists must not interfere with their patients' mental states, but instead accept their thoughts and feelings. Therapists help their patients name, describe, and understand emotions and situate them in current or recent contexts. Thus, the patient's mind is explored by another mind (the therapist's) through interpersonal interactions that are caring and non-threatening, with the therapist's clear explanations using metaphor-free vocabulary, such that the patient fully understands what is happening.

This therapy should not be neglected, because it leverages a neonate's capacity to understand facial emotions and intentions of the primary caregivers and consequently to develop emotional regulations on the ground of these basic experiences essentially made from these imitations (psychic imitation, sensory imitation, and motor imitation). Because language is not yet developed in neonates, these mentalization experiences are able to connect the body and the mind. This opens a very promising avenue for future new psychotherapies, as, for instance, involving facial

retroaction feedback and/or attentional training, such as mindfulness, and/or other emotional regulation strategies (Mikolajczak & Desseilles 2012; Desseilles et al. 2015).

A major blow to primate neonatal imitation and mirror neuron theory

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Abstract: Keven & Akins' (K&A's) compelling new hypothesis explaining the developmental and neural basis of neonatal tongue protrusion has important implications for current understanding of primate imitation and the explanatory value of mirror neurons. If correct, this hypothesis eliminates a major source of evidence for neonatal imitation. I explore the implications this has for mirror neuron research and the arguments building upon them.

Keven & Akins (K&A) offer a novel and convincing hypothesis explaining why neonate primates protrude their tongues in response to various types of stimulation (including adults protruding their tongues at them). Because oral movements required for suckling mature early, they also come under voluntary control early, making tongue protrusion and retraction (TP/R) one of the few motor acts available to newborns. Their hypothesis makes sense in terms of mammalian phylogeny and evolution, and in terms of nervous system development. Essentially, in the same way that "to a man with a hammer everything looks like a nail," early in development the infant's repertoire is so limited that a wide variety of stimuli become affordances for TP/R. These stimuli include seeing others protrude their tongues (putative "imitation"), but also include seeing flashing lights or toys or hearing arousing music. Crucially, K&A's hypothesis explains not just why TP/R is observed early in development, but also explains why it mysteriously disappears shortly thereafter: As the infant's motor repertoire diversifies, a wider response repertoire is available, and the infant moves on to more mature responses. I find K&A's hypothesis and arguments both reasonable and compelling.

Given that TP/R is the only well-replicated "imitative" neonate action from Meltzoff and Moore's (1977) study, and the only action documented more recently in neonates of several nonhuman primate species, K&A's hypothesis should prompt careful reexamination of the literature on neonatal imitation. We know that human babies will eventually become imitators: this is a robust and distinctive feature of *Homo sapiens*. But with other primates the opposite is true, and in adult macaques there is little evidence for imitation.

Meltzoff and Moore's original (1977) study was astounding not because it demonstrated imitation in humans, but because it seemed to show that the connections between human visual perception and motor control were present at birth. But in nonhuman primates, neonatal TP/R remains the only strong evidence we have of *any* form of direct imitation in macaques, and the best evidence for chimpanzees (Ferrari et al. 2006b; Myowa-Yamakoshi et al. 2004; Paukner et al. 2011). To the extent that this apparent evidence does not in fact demonstrate imitation, the only accepted example of macaque imitation has just disappeared.

The significance attached to "imitation" has waxed and waned over time, and a daunting empirical and theoretical literature exists debating and refining terminology (reviewed by Whiten & Ham 1992). In the early days of animal behavior, imitation—"learning to do an act from seeing it done"—was considered a boring low-level form of behavior. This prejudice was perhaps spurred by such English sayings as "monkey see, monkey do" or the German "nachaffen" ("after ape") meaning "to imitate." But

accumulating evidence made clear that much apparent animal imitation is purely in the eye of the human beholder. In many circumstances where we would expect monkeys to imitate each other (e.g., learning to crack nuts with stones by watching a skilled monkey), they fail to show true imitation but rather show simpler behaviors like "stimulus enhancement" (simply observing that rocks and nuts together can lead to food). Each monkey still has to figure out, for itself, precisely how to hold and swing the stones and position the nut (Visalberghi 1987). Such studies led imitation in primates to be seen today as a sophisticated cognitive achievement (cf. Fitch et al. 2010; Visalberghi & Fragaszy 1990; Voelkel & Huber 2000).

Perhaps the biggest reason that evidence for or against monkey imitation is important is that it concerns its implications for the literature on mirror neurons, which were discovered in macaques. Mirror neurons (sometimes called "monkey see, monkey do" neurons [Carey 1996]) are frontal neurons in macaques that fire both when the monkey performs some action and when it sees that same action performed. Such neurons appear to provide a computational substrate for motor imitation. But the catch is that—at the time of the discovery of mirror neurons—the behavioral evidence indicated that macaques do not, in fact, imitate. Although this ugly fact did not stop people from inferring that *human* mirror neurons play a key role in imitation, it was awkward from an evolutionary viewpoint: Just what are these mirror neurons doing in macaques, if not supporting imitation?

For mirror neuron enthusiasts, the 2006 discovery of apparent neonatal imitation in macaques was thus a great relief. Finally, it seemed, a behavioral function for macaque mirror neurons had been found, filling an otherwise uncomfortable lacuna in the theoretical edifice built upon mirror neurons. This is important, given the huge scope of explanations based on mirror neurons today, extending to speech perception, language evolution, autism research, empathy, and other major issues in cognitive neuroscience (skeptically reviewed by Hickok 2014). K&A's hypothesis calls such extensions sharply into question, by offering a simpler explanation of TP/R. Indeed K&A's hypothesis seems preferable to imitative hypotheses because it explains the disappearance of "imitation" during maturation that remains unexplained by the mirror neuron/imitation hypothesis.

The next and crucial step will be to design empirical tests pitting the two hypotheses against one another. I hope that researchers studying primate neonatal "imitation" and mirror neurons will rise to this challenge: The most obvious evidence in favor of K&A would come from single-unit recordings in neonatal macaques, in area F5 where mirror neurons are classically found. If such recordings find no evidence of mirror neuron involvement in the tongue protrusion response, it would be strong evidence in favor of K&A's new hypothesis.

In summary, I applaud K&A for providing a plausible alternative hypothesis for the widely accepted "neonatal imitation" interpretation of the TP/R response, and I am impressed by the breadth and depth of data that they have brought to bear in evaluating and supporting their hypothesis. Although the jury is still out, K&A provide one more reason for skepticism about neonatal imitation in general and monkey imitation in particular, as well as for circumspection about cognitive explanations that rely heavily on mirror neurons.

The case against newborn imitation grows stronger

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Abstract: The claim that human newborns imitate is widely accepted and influential. Yet reliable evidence that newborns match modeled behaviors

is limited, and there is no empirically based explanation of how the knowledge that imitation requires could develop before birth. In their target article, Keven & Akins (K&A) contribute important new evidence to an alternative account of newborns' matching that challenges the newborn imitation claim.

Keven & Akins (K&A) provide an elegant synthesis of research illuminating the developmental course and functional significance of the fetal and neonatal behavior of tongue protrusion/retraction (TP/R). This behavior is particularly interesting because newborn tongue protruding provides a large part of the evidence purporting to show that newborn human infants can imitate. Newborn imitation, in turn, is particularly interesting because of its implications for our understanding of the origins of knowledge (Jones 2017).

Although it is almost never mentioned by developmental psychologists, the claim that newborns can imitate is also a strong claim that we are born already possessed of a good deal of specific knowledge. In particular, it is a claim that we are born with (1) knowledge about at least some parts of our bodies, including how to find them, the movements each can make, and how to make those movements; (2) the same knowledge, but represented differently (e.g., in vision versus in proprioception), about the body parts and movements of others; and (3) knowledge about how the different representations of the two sets of body parts and movements map to each other. These kinds of knowledge appear to be irreducible requirements for the imitation of even the simplest actions. How could they develop before birth? Although it is conceivable that some limited representations of infants' own parts and actions might be constructed by their prenatal movements, infants in the womb can have no experience of the visual information produced by the bodies and actions of others. Therefore, the claim that newborns imitate is a claim that we *inherit* specific knowledge – and complex, multidimensional knowledge at that.

This claim is extraordinary. It is, therefore, surprising that newborn imitation has been so widely, calmly, and uncritically accepted for almost four decades among developmental researchers, and so highly influential in theory building, research, and teaching across a range of disciplines. Throughout this period, new data purporting to show neonates imitating new behaviors have continued to appear. However, there has been little progress in the development of an adequate, empirically supported explanation of where this very early competency might come from and how it might work. The two dominant theoretical proposals identified by K&A – the active intermodal matching (AIM) model (Meltzoff & Moore 1997) and the mirror neuron account (e.g., Simpson et al. 2015) are both very sparse and difficult to test. AIM names a set of separate, necessary components of an ability to imitate, along with the proposed links among them. However, the theory provides no description of the possible mechanisms behind the labels. This theory, then, is not testable in its current form. The mirror neuron explanation of newborn imitation is a relatively recent proposal that by itself is not a complete theory of imitation, and which is not directly testable in human infants. Consequently, the evidence for both theories is still largely confined to repeated demonstrations of newborn behavioral matching.

Although those arguing for the reality of newborn imitation cite neonates' matching of several simple actions (e.g., Meltzoff 2005), independent reviews (e.g., Anisfeld 1996; Ray & Heyes 2011) have concluded that only infant tongue movements are reliably increased in the presence of a model of the behavior. A number of studies have shown that newborns similarly increase their tongue movements as they experience a range of stimuli, including other modeled behaviors (Oostenbroek et al. 2016) and visual, auditory, and somatosensory stimuli bearing no resemblance to a tongue protruding model (Jones 2009). These data suggest that tongue movements are a general arousal response in neonates. The target article supplies a convincing explanation of why tongue protrusions in particular are associated with

moderate increases in arousal. What will the research community make of this?

The arousal explanation of babies' behavior in imitation experiments has met with considerable resistance. There is a danger that the contribution of the present article to our understanding of infant behavior – and, importantly, of what that behavior does or does not tell us about the origins of knowledge – will also be dismissed, because its authors have not directly shown that newborn infants do not imitate tongue protruding/retraction.

We should remind ourselves, then, that given two incompatible explanations of the same phenomenon, we are obliged by the scientific convention of Occam's razor to favor the simplest, testable explanation – that is, the explanation that accounts for the most data using the fewest unsupported assumptions. In the case of newborn infants' response to modeled tongue protrusions, the simplest explanation with the fewest unsupported assumptions is not that newborn babies have inherited the specific knowledge of their own and others' bodies and how each maps to the other that imitation would require. There is no evidence that newborns possess any such knowledge – or for that matter, that they possess an active intermodal matching mechanism, or functional mirror neurons. The simplest explanation for newborns' increasing their tongue movements in the presence of a tongue-protruding model is that the model's behavior is visually interesting and so moderately arousing; that tongue movements – which sometimes take the tongue beyond the infant's lips – are components of newborn suckling, and as such are readily activated with increases in arousal; and that the match between the display that arouses the infant and the infant's arousal response is coincidental. This account is supported by evidence that tongue movements are an arousal response, and now by K&A's documentation of the fetal development of tongue protruding/retraction, which explains the functional place of TP/R in the newborn's repertoire, and why TP/R is easily activated by generalized arousal.

The claim that newborns can imitate is not equally well explained or supported. It is nevertheless woven into the fabric of theories in a range of disciplines beyond developmental science. Those constructing such theories trust that developmentalists have done the work necessary to establish that newborn imitation is real. We have not. It may be time to apply general scientific standards of evidence and acknowledge the likelihood that newborns do not imitate.

There is no compelling evidence that human neonates imitate

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Abstract: Keven & Akins (K&A) propose that neonatal "imitation" is a function of newborns' spontaneous oral stereotypes and should be viewed within the context of normal aerodigestive development. Their proposal is in line with the result of our recent large longitudinal study that found no compelling evidence for neonatal imitation. Together, these works prompt reconsideration of the developmental origin of genuine imitation.

The veracity of neonatal imitation has been debated ever since Meltzoff and Moore (1977) first presented evidence to suggest that newborns imitate adult oral and manual gestures. In an attempt to chart the prevalence of newborn imitation and determine its relationship with later infant development (Suddendorf et al. 2013), we undertook the largest and most comprehensive study of neonatal imitation to date (Oostenbroek et al. 2016). We tested a sample of 106 infants four times, when infants were 1, 3, 6, and 9 weeks of age. A female adult experimenter modeled nine social gestures: four facial gestures (tongue protrusion, mouth opening, happy face, and sad face), two hand gestures (index finger protrusion and grasping), and three vocal gestures (“mmm” sound, “eee” sound, and tongue clicks). Additionally, two nonsocial models were included to test alternative interpretations of neonatal imitation (tube protrusion simulating tongue protrusion, and box opening simulating mouth opening) (Jacobson, 1979; Jones 1996). Across this range of gestures, there was no sign that infants selectively imitated any of the modeled gestures.

In our analyses of infants’ responses to these models (as outlined above), we replicated some previous findings in restricted subsections of the data. Specifically, when we used the common cross-target procedure of comparing infants’ tongue protrusions in response to the matching model with their tongue protrusions in response to the control model of mouth opening (see Meltzoff & Moore 1977), we found that infants produced significantly more matching responses than non-matching responses at 1 and 9 weeks of age. However, this effect disappeared when we used other gestures as the control model. Because there is no a priori reason to favor mouth opening as the comparison control model over any other control model (e.g., happy face), these cross-sectional findings also do not provide evidence of newborn imitation. This suggests that failure to include adequate control conditions or to test infants across multiple time points in previous studies has resulted in the false impression that infants selectively copy tongue protrusions, thereby perpetuating the idea that newborn imitation exists.

In their target article, Keven & Akins (K&A) offer a novel explanation for why tongue protrusion in particular may be falsely identified as imitation. They argue that what others have interpreted as imitation may be spontaneous oral activity – with tongue protrusion being characteristic – arising from maturation of the infant’s respiratory and digestive systems. K&A not only offer a rationale for why newborns might engage in tongue protrusion behaviors at such high rates, but also provide a compelling and consistent argument for why this gesture may decline after the first 3 months of life. We welcome this contribution because it provides another reason why previous data claiming evidence of neonatal imitation, and tongue protrusion imitation in particular, should be interpreted with caution.

In their article (sect. 7, para. 2), K&A cite our research while discussing the frequency of newborn behaviors. They state, “Of these ‘early’ stereotypies, TP/R [tongue protrusion and retraction] and MO/C [mouth opening and closing] and index finger protrusion are produced with the highest frequencies during the first week after birth” (Oostenbroek et al. 2016). We take this opportunity to clarify that the high frequencies of these behaviors do not provide evidence of imitation. Although 1-week-old infants in our sample engaged in higher levels of tongue protrusion, mouth opening, and index finger protrusion than any of the other modeled gestures at this age, they produced these behaviors as often in response to many of the control models as they did to the corresponding matching models. K&A’s alternative explanation for the “imitation” of oral gestures, coupled with our comprehensive, longitudinal data, supports the conclusion that imitation does not exist in the newborn period. Rather, its apparent expression is a result of the maturation of developmental mechanisms that may have nothing to do with social learning.

After more than 30 years of controversy over its existence in the newborn period (see Oostenbroek et al. 2013; Ray & Heyes 2011; Simpson et al. 2014a; Suddendorf et al. 2013) driven largely by

studies using cross-sectional designs and only tongue protrusion as the model gesture, K&A’s article, along with our findings, necessitates a reframing of imitation research. These data suggest that neonatal imitation is an illusion and should encourage new perspectives and research goals. There is no longer a compelling empirical basis for the idea that human neonates imitate. Developmental scientists should reconsider the origin of imitation, and explore novel hypotheses about the functions of newborn oral behaviors, starting with K&A’s well-articulated and compelling account.

Mommy or me? Who is the agent in a sense of agency in infant orofacial stereotypies?

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Abstract: That neonates imitate is an assertion that lacks supporting evidence. Orofacial stereotypies are critical to optimizing food rejection. Matching of tongue-protrusion is not imitation, but a manifestation of the infant’s arousal by the modeler’s exhibition of the same behavior. The support for the nativist assertion that newborn infants imitate is not compelling, and we should proceed on the assumption that they do not.

Keven & Akins (K&A) conclude correctly that orofacial stereotypies are critical to the development of aerodigestion in neonates and are unlikely to co-occur with imitative behavior. Much has been made of facial imitation at birth. Neonates project their tongues in reaction to scientists doing the same, suggesting that proper imitation starts at birth. Fetuses have been protruding their tongues long before birth and postnatally. One needs, therefore, to address automatic imitation (mimicry) rather than proper imitation. The purpose of tongue-protrusion relates more to food being too hot or unpalatable. For the neonate, tongue-protrusion optimizes food rejection, a process commenced in the womb. Tongue protrusion (generally accompanied by other forms of grimacing and back extending) is an effective means of rejecting food and signaling the caregiver that something is wrong. If neonates and infants also increase tongue protrusions when adults simulate a happy face or finger point, then it is not imitation, but likely excitement at seeing an adult perform an interesting task. Imitation is not an innate behavior but tongue-protrusion is, and their combined response to environmental cues postpartum is learned in a baby’s first months. Infants learn to imitate others based on observing others imitate them. Neonates are not born with the ability to copy others; they acquire that skill during the first months of life (cf. Leisman et al. 2012; Melillo & Leisman 2009).

The widely accepted view that newborn infants imitate lacks supporting evidence. Existing data suggest that infants do not imitate until their second year; imitation of different kinds emerges at different ages. The evidence is consistent with a dynamic systems account in which imitation ability is not an inherited, specialized module but is the emergent product of a system of social, cognitive, and motor components, each with its own developmental history.

The necessity of an internal description or representation of a motor response helps explain why imitation of orofacial gestures is such a good candidate for imitation via a mirror system. It is well-known that fetuses perform mouth-opening and closing and tongue protrusion (Longo 2008; Precht 1986). These gesticulations are part of the neonate’s behavioral repertoire at birth. Neuroanatomical evidence shows that the corticobulbar tract is

already myelinated, innervating mouth and tongue (Sarnat 2003), enabling automatic elicitation of the observed response. Whereas some claim that these behaviors are reflexive and would not necessitate an internal representation, Lepage & Théoret (2007) noted that imitative behaviors are automatic rather than reflexive and demonstrate that orofacial gestures follow visual and auditory stimuli. A reflexive response, however, would not be elicited by more than one modality. Support for neonatal imitation suggests that infants are more likely to match actions after each has been presented over time (~40 sec), rather than instantly (Anisfeld 1991). This finding is more consistent with a mirror system where activation is expected to build up gradually over time as the gesture is modeled, as opposed to explanations claiming that the behavior is merely reflexive. The reflex would be present at birth, but gesture modeling would be built over time.

Data intimate that infant imitation is nonreflexive and possesses a developmental course similar to many primitive reflexes, increasing until approximately 2 months of age, declining and virtually disappearing by 5 months of age (Fontaine 1984). During this same timeframe, primitive reflexes are gradually inhibited (McGraw 1943), signifying that similar cortical inhibitory processes may suppress spontaneous imitation. As automatic prompting of orofacial gestures becomes suppressed with age, imitation does not vanish. Instead, it becomes subject to voluntary control. This result is seen in adults with frontal lobe lesions with impaired inhibitory control, who display compulsive imitation (Lhermitte et al. 1986).

One nativistic explanation implies that imitation is a unitary competency—a dedicated behavior having evolved as a unit (Ferrari et al. 2006a). It has been suggested that neonatal imitation is an inherited, specialized neurological mechanism for imitative behavior in human infants and adults (e.g., Iacoboni & Dapretto 2006). A second account of the origins of imitation (cf. Gottlieb 2007) suggests that the capacity to match others' behaviors is not present at birth but emerges during the second year continuing to mature over time, with no heritable specialized mechanism. Instead, imitation arises from the infant's attainment of cognitive, motor, and social skills. Differing explanations of the development of imitation are conceivable because the literature provides inconsistent reports that can be variously interpreted.

Neonatal imitation is key in developmental cognition because it asserts a core nativist position for the origins of knowledge. Neonatal imitation is achievable only if infants receive significant awareness of their bodies or agency. It is imperative to ask whether support for this claim is compelling. In newborn imitation experiments, infants are typically exposed to two different behaviors. In a majority of cases, one is tongue-protrusion, the other being mouth-opening. Infants outside of imitation experiments normally produce both behaviors. The literature reports that newborns selectively increase their production of each behavior over baseline after seeing that particular behavior modeled (e.g., Meltzoff & Moore 1983).

Anisfeld (cf. 2005) assessed numerous studies of neonatal imitation, which had tongue protrusion as a focal behavior. Only tongue protrusion was consistently matched by newborns in different studies. If neonates imitate only one behavior, then matching may be a consequence of arousal and not of imitation. Anisfeld (1996) and Jones (1996) reported that infants increased rates of tongue protrusion when interested or aroused by stimuli (e.g., flashing colored lights) not resembling human tongue protrusion. Humphrey (1970) showed that neonates manifested tongue protrusion in response to palm-touching, approaching and receding pens, small balls, and short segments of *The Barber of Seville* overture (Jones 2006a). The results corresponded with patterns in imitation experiments, suggesting that all stimuli are arousing; tongue protrusion is a common response of neonates to numerous arousing stimuli in different sensory modalities.

Therefore, it is likely that newborns' matching of tongue protrusion is not imitation but a manifestation of the infant's concentration in or arousal by the modeler's exhibition of the same behavior.

The support for the nativist assertion that newborn infants imitate is not compelling, and we should proceed on the assumption that they do not.

“What” matters more than “Why” – Neonatal behaviors initiate social responses

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Abstract: Newborns are born into a social environment that dynamically responds to them. Newborn behaviors may not have explicit social intentions but will nonetheless affect the environment. Parents contingently respond to their child, enabling newborns to learn about the consequences of their behaviors and encouraging the behavior itself. Consequently, newborn behaviors may serve both biological and social-cognitive purposes during development.

In their article, Keven & Akins (K&A) describe newborns' tongue protrusion and retraction (TP/R) as an early emerging orofacial stereotypy that serves to facilitate the activity-dependent development of core aerodigestive functions. This view suggests that TP/R is not an imitative response and emphasizes that development is continuous from the prenatal to the postnatal period (Einspieler et al. 2008; Precht 1984). We agree with this view but would like to comment on the terminology of “stereotypies” used in the target article and discuss additional considerations regarding the learning opportunities initiated by neonatal behavior in a social context.

First, referring to TP/R movements as stereotypies is misleading. This terminology is commonly associated with behaviors that lack variability and may be a sign of, or predictor for, various developmental disorders (Goldman et al. 2009; Matson et al. 2009). In contrast, TP/R movements show considerable variability and have a clear developmental relevance as discussed by K&A. Consequently, TP/R movements might not bear characteristics of motor stereotypies from a neurodevelopmental or clinical perspective. Therefore, we propose referring to TP/R more generally as “movements” or “behaviors” to avoid a potential misunderstanding.

Second and most importantly, although behaviors driven by endogenous central pattern generators (CPGs) are critical for development, the exogenous social consequences following neonatal movements need to be considered as well. Infants do not develop in a vacuum but are born into a rich social environment that responds dynamically to their actions. In fact, maternal engagement is synchronized and strongly influenced by the newborns' behaviors (Feldman 2007). Specific behaviors of the mother (e.g., “motherese,” face-to-face exchanges, affectionate touch) are genetically determined but also dynamically adjust to environmental factors (Keller 2003; Leckman et al. 2004). For example, when responding to infant's cooing, mothers not only heighten their fundamental frequency, but also introduce pauses that facilitate learning about turn-taking in communication (e.g.,

Stevenson et al. 1986). These examples demonstrate that the child's (motor) behavior affects how the parent interacts with the child. These changes result in "developmental cascades" (Masten & Cicchetti 2010) where the child's behavior triggers a new or different response in the parent that may then facilitate subsequent development across domains.

Evidence for such developmental cascades also comes from older infants: Mothers offer different verbal feedback to sharing bids from crawling infants than to sharing bids from walking infants (Karasik et al. 2011; 2014). Therefore, we believe that a caregiver's observations of neonatal movements (including TP/R and other CPG behaviors) influence the caregiver's responses and interactions with the child. Neonatal behaviors can initiate developmental cascades by triggering a certain response in the caregiver (such as a vocalization or imitation by the caregiver) and consequently serve a social function, even if this was not the "intention" of the child. Put differently, although the newborn may not "imitate" the parent, what matters more is how the parent reacts and responds to the child's behavior.

Finally, we would like to also note that infants (including newborns) are sensitive to contingencies present in their environment and adjust their own behaviors accordingly. For example, newborns adjust their sucking rate (an aerodigestive behavior just like TP/R) in order to elicit a preferred stimulus such as a speech sound or a stimulus that is contingent on their own sucking rate (DeCasper & Carstens 1981; DeCasper & Fifer 1980; Floccia et al. 2000; Vouloumanos & Werker 2007). Older infants learn the contingencies between movements of their limbs such as arms or legs and changes in their environment (Needham et al. 2002; Rovee & Rovee 1969). In these examples, the infants' initial motor activity (either sucking or limb movements) is not aimed at eliciting a certain outcome. However, the repeated exposure to contingencies between motor behavior and environmental response leads the infant to increase the motor activity in order to re-elicite the response (e.g., kick their legs more to make a mobile hanging over a crib move more). Consequently, it is possible that newborns may be able to also adjust their rate of TP/R behaviors in response to observed behaviors of their parent. Together, these two mechanisms can act as a positive feedback loop: Newborns engage in TP/R, parents notice and respond, newborns increase TP/R behavior, parents respond more, and so on.

Consequently, TP/R behaviors may well have a secondary impact on socio-cognitive development during dynamic and contingent parent-child interactions. One example for how motor activity can affect socio-cognitive development via similar feedback loops and cascades is pointing. The motor pattern underlying pointing (i.e., extending the index finger) is present already before birth (e.g., Einspieler et al. 2012; Marschik et al. 2013). However, the use of pointing for communicative purposes emerges only around 9 to 14 months of age (Liszkowski et al. 2012). Before the infant uses pointing to communicate, parents inevitably perceive pointing as a communicative signal from the infant and respond to the pointing bid. Over repeated observations of the caregivers' reaction to pointing, infants eventually learn to use pointing communicatively (Bates et al. 1975; Carpendale & Carpendale 2010; Vygotsky 1978). Following the same logic, TP/R does not need to be intended as imitation by the newborn, but may provide the newborn with opportunities to learn about imitation through observation of the parent's response to this repeating behavior.

In summary, the mechanisms of the developing system are highly interconnected. One behavior, such as TP/R may exist to serve a particular biological purpose. However, during the dynamic exchanges with the environment this behavior will inevitably be used for other purposes as well. In particular, socio-cognitive functions such as communication and language are secondary functions to respiration and orofacial functions for food intake. A comprehensive account of infant development needs to consider that seemingly simple behaviors such as TP/R may serve such a dual purpose: endogenously generated at first

and at the same time facilitating socio-cognitive development via social interactions and responses from the environment.

Do innate stereotypies serve as a basis for swallowing and learned speech movements?

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Abstract: Keven & Akins suggest that innate stereotypies like TP/R may participate in the acquisition of tongue control. This commentary examines this claim in the context of speech motor learning and biomechanics, proposing that stereotypies could provide a basis for both swallowing and speech movements, and provides biomechanical simulation results to supplement neurological evidence for similarities between the two behaviors.

Keven & Akins (K&A) suggest that neonate tongue protrusion and retraction (TP/R) participates in the acquisition of tongue control: Specifically, it "begins as an activity 'for' tongue protrusion itself, that tongue protrusion begets tongue protrusion of a 'more better' kind" (sect. 6.3, para. 1). They discuss this primarily in a neurological context, whereby spontaneous TP/R leads to incremental circuit formation in central pattern generators (CPGs), fostering the transition from "uncertain movements" to "robust rhythmic motor sequences." Neuromuscular primitives used as starting points for more complex movements are not unique to the aerodigestive tract, nor to humans: Wolpert et al. (2001) noted that innate motor behaviours are common across species, allowing faster acquisition of motor skills by providing a starting point for motor learning, for which behavioral evidence has been found in human and animal locomotion (Dominici et al. 2011).

This refinement of innate, spontaneous actions for use in more complex motor behaviours mirrors a largely untested but appealing hypothesis in speech research which proposes that phylogenetically encoded structures like swallowing and suckling may bootstrap speech learning (e.g., MacNeilage 2008; Studdert-Kennedy & Goldstein 2003). This proposal appears plausible in view of the accumulated evidence that digestive and speech movements share not only kinematic similarities (Green et al. 2000), but also many of the same neurological structures. Both types of movements exhibit large areas of shared brain activation (e.g., Martin et al. 2004), as well as similar critical periods in early development and correlations between disorders in each domain (McFarland & Tremblay 2006). Clinical studies have shown that language impairment is a predictor of previous feeding and swallowing difficulties (Malas et al. 2017) and that treatment of dysphagia has resulted in concomitant improvements in dysphonia (LaGorio et al. 2008).

The bootstrapping proposal is based on the idea that speech movements share more than kinematic or neurological similarities with digestive movements, but rather that there are at least some core speech movements which are direct ontogenetic adaptations of preexisting digestive movements. This implies that aspects of

the two activities must plausibly be driven by common specific sets of muscle activations (Gick & Stavness 2013). If we represent muscle activation space as a high-dimensional space where each muscle has a corresponding dimension whose value is that muscle's activation level, learning speech movements can be modeled as a search for points in this space that satisfy task-specific criteria relevant to the speech learner. The dimensionality and size of this space are large enough to pose significant problems for an unstructured search, even for a single speech movement in isolation: The sets of activations that result in a solution for a given task are few in number relative to all possible sets of activations (see Gick et al. 2017), and muscle activation is difficult to predict due to the number of redundant solutions for a given task (Loeb 2012). Factors such as muscle contraction dynamics, tissue mechanics, tissue incompressibility, and tongue-palate contact also mean that task-level similarities do not necessarily imply similar activations. Establishing such similarities adds significant weight to the argument that primitives help constrain possible muscle activation patterns for speech learning.

We explored these ideas using the 3D biomechanical modelling platform ArtiSynth (www.artisynth.org; e.g., Gick et al. 2014; Stavness et al. 2012) in the context of tongue bracing, where active muscle support keeps the sides of the tongue in almost constant contact with the upper molars during speech (Gick et al. 2017). Simulations were conducted to examine the muscles activated for various types of tongue-palate contact. All possible muscle combinations were activated at three activation levels (0%, 20%, 50%) out of a group of 10 speech and swallowing muscles: superior and inferior longitudinal, transverse, verticalis, hyoglossus, mylohyoid, styloglossus, and posterior, medial, and anterior genioglossus. This generated approximately 60,000 activations. Virtual contact sensors were positioned on the hard palate and upper teeth of the model to detect tongue contact. We partitioned the activation space into four different contact types (Fig. 1). Only about 2% of the activations matched any of these. "Lateral" indicates tongue contact on the sides of the palate, as for speech bracing. "Anterior" indicates contact in the anterior region of the palate, as in the production of the sound [l]. "Anterior-lateral" indicates simultaneous lateral and anterior contact, as in the production of the sound [n]. "Swallowing" indicates lateral, back, and mid-contact, representing the end of the oral transport phase of swallowing, immediately after the tongue has moved the

bolus into the hypopharynx. See Gick et al. (2017) for a detailed description of a similar simulation with different analysis.

Results indicate that activations resulting in swallowing contacts were a subset of activations that resulted in tongue bracing contacts. The superior longitudinal and mylohyoid muscles played the most significant roles in both swallowing and bracing contacts, but with additional activations occurring to produce the more complex tongue shapes required by bracing contacts such as depressing the midline and raising the tip. We also found that the activations that resulted in swallowing contact were contiguous with clusters of activations resulting in bracing contact, indicating similar activations. This is shown in Figure 1 using the dimensionality reduction technique t-Distributed Stochastic Neighbor Embedding (t-SNE; van der Maaten & Hinton 2008). The t-SNE technique maps from high-dimensional to low-dimensional space using an optimization function that prioritizes maintaining distances between each point and its neighbours.

Although it has become increasingly well established that swallowing and speech movements are neurologically related, it does not immediately follow that they have similar neuromuscular activation patterns: The nonlinearity of the muscular activation space offers no guarantees that task-level similarities necessarily translate into similarities in activation space. The simulations presented here suggest similarities in neuromuscular activation between tongue bracing and swallowing, filling the gap between previous kinematic and neuroimaging findings. Such biomechanical simulations, taken in the context of proposals such as that of K&A, will provide an essential part of the evidence for establishing the role of innate stereotypies like TP/R in facilitating the development of semi-closed movement routines such as swallowing as well as serving as a basis for learned speech movement.

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Elements of a comprehensive theory of infant imitation

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Abstract: Imitation is central to human development. Imitation involves mapping between the perception and production of actions. Imitation after delays implicates preverbal memory. Imitation of people informs us about infants' processing of social events. A comprehensive theory needs to account for the origins, mechanisms, and functions of imitation. Neonatal imitation illuminates how the initial state engenders and supports rapid social learning.

Keven & Akins (K&A) provide a theory about the development of infant suckling, swallowing, and motor stereotypies. As they acknowledge, it is not a theory of infant imitation. Here are six key empirical findings that need to be accounted for by any comprehensive theory of infant imitation.

1. Infant imitation is selective and specific. K&A agree with Meltzoff and Moore's findings that if you poke out your tongue at neonates, they will do so in response. However, K&A do not account for our parallel finding that if you show other control gestures – gestures by the same person, at the same distance, moving at the same rate – infants do *not* respond with tongue protrusion. Experiments making this direct comparison provide a consensus that adult tongue protrusion is the strongest elicitor of the infant tongue-protrusion response (reviews by Anisfeld 1991; Meltzoff & Moore 1997; 1999b; Nagy et al. 2013; Ray & Heyes

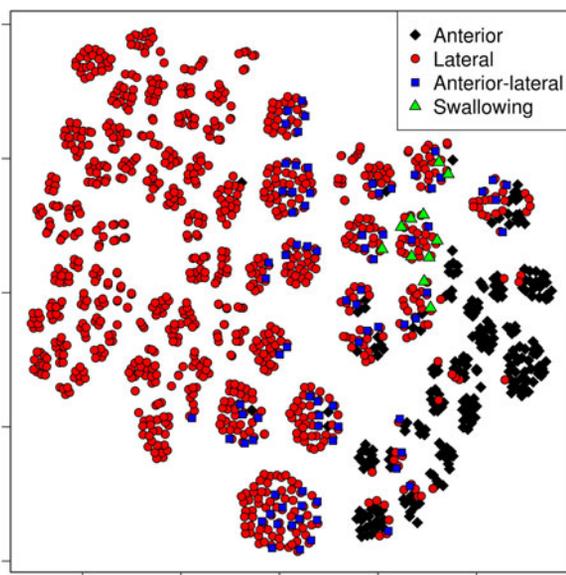


Figure 1 (Mayer et al.). A two-dimensional t-SNE plot of the 2% of the activation space that matched one of the target contact types.

2011; Simpson et al. 2014a). Motor stereotypies alone cannot account for this selectivity.

2. Infants imitate manual movements as well as facial movements. K&A's theory of the aerodigestive system does not explain the imitation of manual movements. Echoing the first point on selectivity, neonates imitate different types of manual movements (Meltzoff & Moore 1977; Nagy et al. 2014; Vinter 1986). Piaget's (1962) classic book showed accurate imitation of hand movements in 1- to 4-month-olds. K&A "predict" that both Piaget's and the newer findings should not occur in infants this young.

3. Infants imitate from memory. K&A acknowledge that infants often respond after a delay of a few seconds in experiments of imitation. However, they do not discuss how their theory would handle findings based on long-term memory. Meltzoff and Moore (1994) showed young infants' tongue protrusions on one day and then presented them with a passive face on the next. Infants produced significantly more tongue protrusions when they saw this passive face after a 24-hour delay than did control infants (who did not see the tongue protrusions the day before). This suggests that young infants have a memory for facial actions. Within the first year of life, infants also imitate object-directed acts based on memory (e.g., Klein & Meltzoff 1999; Meltzoff 1988). A comprehensive theory of infant imitation needs to explain imitation from memory.

4. Infants can vary their tongue movements prior to 4 months of age. K&A argue that infants have no directed control of their tongues before 4 months of age. All tongue movements are purported to be the stereotypic thrust/retraction involved in suckling. Three empirical findings suggest that infants' competence exceeds this. First, infants imitate *different kinds* of tongue movements (Meltzoff & Moore 1994). Second, prior to 4 months of age, infants spontaneously produce diverse cooing sounds, which require tongue movements markedly different from suckling and tongue stereotypies. Third, infants imitate speech sounds by 20 weeks of age as documented by phonetic transcriptions and spectrographic analyses (Kuhl & Meltzoff 1996). The tongue shapes and positions used for imitating sounds like "ah" and "uu" differ from each other and from tongue stereotypies. Different sounds elicit different lip and tongue movements.

5. Infant imitation does not fit the timetable of motor stereotypies. As Piaget (1962) reported, vocal and manual imitation are expanding, not contracting, at the age that K&A predict a "drop out" of infant imitation based on the motor stereotypies literature. Furthermore, even though infants may not systematically imitate tongue protrusions under one type of experimental design during this time, they *do* succeed when the design is changed. This suggests a constraint on performance, not a lack of competence. Meltzoff and Moore (1992) argued that by 12 weeks of age infants have learned expectancies about face-to-face interactions, and they remember past encounters with a person. When a person switches from demonstrating one facial gesture to another, there is response carryover. Accordingly, we conducted a study with a new design: Two distinctly different adults were used to demonstrate gestures to infants, and each modeled a different gesture. In this case, we observed significant imitation of each adult's gesture. Our active intermodal mapping (AIM) theory proposes that infant facial imitation fits within a larger social context involving face processing and the individuation of people (Meltzoff & Moore 1992; 1997; 1999b). Although agreeing that the sensorimotor context is important, I maintain that infant memory and the *social context* must also be considered when explaining developmental change in imitation.

6. The role of prenatal movements. One central aspect of Meltzoff and Moore's (1997) AIM theory is that infants' prenatal body movements contribute to postnatal imitation. We argued that such activity is a mechanism by which infants build up an "act space" of possible movements of the lips, tongue, hands, and other body parts. Having produced the movements prenatally, infants are in a better position to make sense of the visual stimulus produced by others and map it to their own productions. Meltzoff and Moore (1997) provided a detailed model for how

infants link the perception and production of matching acts. We described the "metric of equivalence" that underwrites infants' mapping of seen body transformations to those they feel themselves produce. Studies using infant neuroscience techniques, such as electroencephalography (EEG), are providing new insights into this process, including the role of somatosensation and infant neural body maps (Saby et al. 2013; 2015).

The target article concludes by saying that developmental psychologists habitually adopt a simple black/white nature versus nurture distinction. The field of developmental science, however, left behind that dichotomy more than 40 years ago, and has integrated perceptual learning, motor development, neuroscience findings, and both prenatal and postnatal experience into theories of infant development (Marshall & Meltzoff 2014; 2015; Meltzoff & Moore 1997; and many others). That is the larger context in which a comprehensive theory of infant imitation should be situated.

Beyond aerodigestion: Exaptation of feeding-related mouth movements for social communication in human and nonhuman primates

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Abstract: Three arguments are advanced from human and nonhuman primate infancy research for the exaptation of ingestive mouth movements (tongue protrusion and lip smacking) for the purposes of social communication: their relation to affiliative behaviours, their sensitivity to social context, and their role in social development. Although these behaviours may have an aerodigestive function, such an account of their occurrence is only partial.

Keven & Akins (K&A) view infant mouth movements, such as tongue protrusion (TP), as part of the system for regulating ingestion in relation to breathing. They view these behaviors as stereotyped, not goal-oriented, and unresponsive to stimulation, albeit varying with arousal. In contrast, we present three arguments from research on early parent-infant relationships, including cross-species and clinical samples, for the social function of such mouth movements: their relation to affiliative behaviors, their sensitivity to social context, and their role in social development.

1. Relationship between aerodigestive and affiliative behaviours. Observational studies of human and nonhuman primate (NHP) infants are remarkably consistent in showing

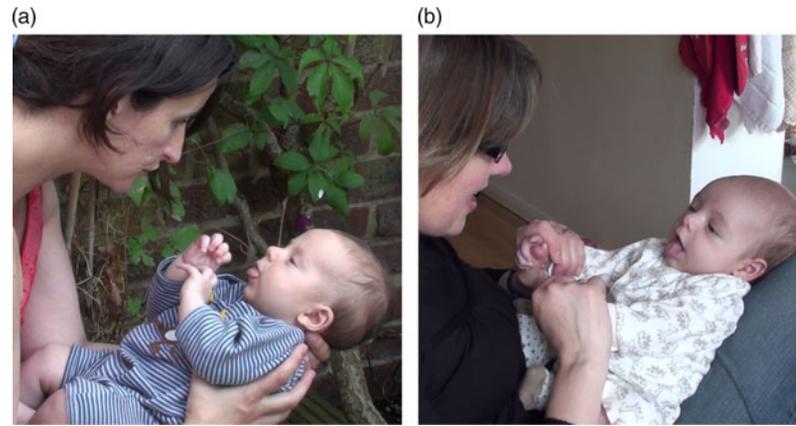


Figure 1a and 1b (Murray et al.). Infant tongue protrusion, with and without arm/hand movements, during face-to-face interaction.

that mouth movements originating in ingestion nevertheless have distinct, communicative significance (Trevarthen 1979; Van Hooff 1962). These include TP in humans and lip smacking (LS) in NHPs, including rhesus macaques. In each case, the behaviour rapidly becomes prominent in early parent-infant interactions (Ferrari et al. 2009a; Trevarthen 1974; Murray et al. 2016), and is highly organized, systematically co-occurring with other, clearly affiliative behaviors. For instance, in humans, TP in the first two months is associated with smiling, wide mouth-opening, and positive vocalizations—a cluster of expressions termed “prespeech” (Fig. 1; Murray et al. 2016). These expressions occur during direct gaze to the adult’s face, often accompanied by arm waving with open hand movements (Fig. 1a) (Lavelli & Fogel 2002; 2005; 2013; Supplement SII; Trevarthen 1974; 1979).

In macaques, LS similarly appears as part of social encounters, and co-occurs with direct gaze and proximal contact with the parent; even newborns actively solicit their mothers to interact using LS (Dettmer et al. 2016; Ferrari et al. 2009a). The time course of TP and LS is strikingly similar in humans and monkeys, increasing in frequency over the first few weeks, and then declining with the reduction in face-to-face interactions and the infant’s growing exploration (Ferrari et al. 2009a; Trevarthen & Aitken 2001). Notably, each behavior is functionally autonomous with respect to digestive chewing—whether in terms of its co-occurrence (TP [Murray et al. 2016]; [Supplement SII]) or developmental trajectory (LS [Ghazanfar & Takahashi 2014]).

2. Sensitivity to social context. Infant TP and LS are highly sensitive and responsive to others’ interactive behavior. In addition to the consistent evidence from well-conducted studies for neonatal imitation of these gestures (Simpson et al. 2014a), human research using experimental perturbations shows that if normal face-to-face contact is broken by the parent adopting a still, blank face, infants show less positive social engagement (Mesman et al. 2009), including reduced TP (Murray & Trevarthen 1985). This effect is not simply a function of lack of parental stimulation lowering infant arousal, because similar reductions in engagement (and TP) occur when infants see their parent in a noncontingent versus identical contingent face-to-face interaction (Murray & Trevarthen 1985; Nadel et al. 1999). Disturbances in clinical populations also demonstrate the influence of variations in face-to-face interactions on human infants’ social responses. For example, 2-month-olds of socially anxious mothers show low levels of social engagement themselves, including TP, an effect that is mediated by their mothers’ reduced positive social signals (Murray et al. 2007). Similar effects are found for infants of depressed mothers (Murray et al. 1996). Parallel findings to the human experimental studies emerge from NHP research:

specifically, infant macaques reduce their LS and social attention when presented with a still face versus an active interactive experimenter; and they show more LS and attention when an experimenter interacts with them using contingent, imitative mouth responses rather than similarly prominent, but noncontingent, repetitive mouth movements, despite the latter condition providing more overall stimulation (Scelafani et al. 2014).

3. Role of infant TP and LS in later social development. Human observational studies show that parents respond positively to early infant signs of social engagement or “prespeech,” imitating and affirming them, and according to their communicative and playful significance (Lavelli & Fogel 2002; Trevarthen 1979; Murray et al. 2016; Supplement SI2). In turn, the further development of these infant behaviours is promoted by parental facial responsiveness (Murray et al. 2016), so that cultural differences in its prevalence (e.g., as between U.S./European and some African populations) predict somewhat different infant social trajectories (Kärtner et al. 2010; Wörmann et al. 2012). Face-to-face interactions between mother and infant macaques also influence the development of infant social functioning: Monkey neonates that receive more facial responsiveness from their mothers spend more time in social contact with other monkeys at 2 months of age, and they initiate more social interactions at 5 months (Dettmer et al. 2016). That this effect is driven by experience of face-to-face interactions, rather than physical contact, is indicated by the finding that nursery-reared infants receiving mutual gaze and LS from a human caregiver subsequently show more social interest and social contact with peers than infants receiving either handling without gaze and LS, or standard nursery care. Notably, infant experience of early social interactions influences putative mirror neuron system responses, with infant monkeys raised with their biological mothers already demonstrating more mu desynchronization during observation of LS at 3 days postpartum compared to those raised apart (Vanderwert et al. 2015). Such impact suggests a preparedness of the neonate brain to respond to social cues by harnessing aerodigestive behaviours, with a rudimentary mirror system rapidly refined by early experience. This may increase neural sensitivity to socially relevant stimuli such as LS, and thereby confer significant benefits for infants’ navigation of the complex social world into which they are born (Vanderwert et al. 2015). Recent research with human children similarly suggests mirror system involvement in the processing of facial expressions from a young age (Rayson et al. 2016; 2017).

In sum, we provide evidence from naturalistic, experimental, and clinical studies to show that infant mouth movements like TP/LS are complex and sensitive to context, and are fundamentally embedded in social interactions early in development, with longer-term significance for social functioning. Therefore, while

both TP and LS may indeed have aerodigestive origins, they have also been exapted for uniquely social purposes.

SUPPLEMENTARY MATERIALS

To view supplementary material for this article, please visit <https://doi.org/10.1017/S0140525X16001941>

Infant orofacial movements: Inputs, if not outputs, of early imitative ability?

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Abstract: According to Keven & Akins (K&A), infant orofacial gestures may not reflect imitative responses. Here, we emphasise that these actions nonetheless represent a significant feature of the infant's early sensorimotor experience, and therefore may play a key role in the development of imitative capacities. We discuss how the ideas proposed in the target article could contribute substantially to experiential accounts of imitation.

Keven & Akins (K&A) have contributed an important new perspective to a growing body of literature that has challenged long-standing assumptions regarding the existence of innate imitative ability in infants (Jones 1996; Oostenbroek et al. 2016; Ray & Heyes 2011). We agree with their assertion that infant orofacial "gestures" likely do not in fact arise as a consequence of imitation of others' actions. Nonetheless, evidence of imitation in slightly older children is indisputable, and rejection of a nativist interpretation necessitates adequate alternative explanations of such proficiency. We believe there is now a pressing need for consideration and investigation of such alternative accounts. In this commentary, we would specifically like to advocate the importance of understanding how early experience is involved in the development of imitative ability.

Early work by Piaget (1962) suggested imitation developed in a step-wise manner over the first 2 years, a finding now supported by more systematic research (Jones 2007). Some theoretical models have proposed that this developmental trend is scaffolded by sensorimotor experience; for example, when an infant observes their own actions, or when a caregiver's actions correspond to those of the infant. According to this view, this experience builds associations between sensory and motor representations of the same action that will later facilitate imitation (Brass & Heyes 2005; Ray & Heyes 2011). It follows from these assumptions that the stereotypic actions discussed by K&A are likely to play a significant role in the development of these associations. Indeed, evidence suggests that caregivers frequently imitate infant action (Flynn et al. 2004; Pawlby 1977), and stereotypes may increase during caregiver interaction (Thelen 1981a). Opportunities for caregiver imitation may, therefore, largely consist of rhythmic stereotypes. These imitative interactions could provide the infant with rich sensorimotor experience critical to the formation of associations which eventually underpin their own imitative capacities. Therefore, orofacial stereotypes in infancy might more accurately be viewed as inputs into, rather than outputs of, early imitation.

Our own work on action imitation in older children has found that the likely extent of sensorimotor experience of synchronous

activity appears to be related to the automaticity of imitative responses (O'Sullivan et al., *under review*). Although such effects have yet to be identified in infants, we would expect that nascent imitative abilities would be similarly affected by the aggregated experience of correspondences between sensory and proprioceptive feedback associated with particular actions. To conclusively demonstrate that sensorimotor experience is a key component of imitative development, researchers must document naturally occurring sensorimotor experience and its implications for imitation throughout the first year. The study of behavioural stereotypes offers valuable groundwork that could inform the approach taken within such an enterprise.

A systematic developmental approach to the study of infant stereotypes and their environmental triggers could also considerably strengthen K&A's argument, as well as augmenting our understanding of the development of imitation. We are sympathetic towards the notion that apparently imitative responses in neonates may in fact be an artefact of stereotypic behaviour triggered by arousing stimuli. Thelen's (1979; 1981a) observational studies of rhythmic stereotypes in infancy (cited in the target article) have provided important groundwork in this respect, identifying a wide range of stereotypes and some apparent releasers. However, to further elucidate the reasons for apparently imitative correspondences during infancy, experimental approaches (similar to those used in neonatal imitation studies) could be used to systematically investigate the responses elicited by a comprehensive suite of actions modelled by a caregiver (including, importantly, those identified as common rhythmic stereotypes with different peak postnatal frequencies). Arousal theories propose that correspondences between the actions of model and infant are found in studies of neonatal imitation because the model's actions tend to be arousing, and the infant's actions are developmental stereotypes which would increase in response to any arousing stimulus. If this is the case, it should follow that any stimulus known to release a particular stereotype during a specific postnatal phase of development should also trigger the production of other stereotypes during other phases of development (i.e., in accordance with their documented peak production frequencies). Such evidence would corroborate the conclusion that correspondences are coincidental, rather than imitative responses. Nonetheless, assuming a role for experience in the development of imitation, one might also expect that, over the course of development, the specific actions produced by the infant should show an increasing tendency to match those of the model across the full range of behaviours (and taking into account expected production frequencies).

Finally, we would also like to highlight the implications of the argument in the target article, along with an experiential account of imitative ability, for understanding the social role of imitation. A rich literature has explored how imitation in children and adults is associated with affiliation towards imitators (Chartrand & Bargh 1999; Over et al. 2013). It has been suggested, likely because of assumptions about the innateness of imitative ability, that this is an adaptive response which has been subject to evolutionary selection pressure (Lakin & Jefferis 2003). However, K&A have highlighted how behavioural stereotypes are linked with arousal in infants (Jones 1996; Nagy & Molnar 2004), and as proposed in the foregoing, these stereotypes may also provide opportunities for imitative interactions. Therefore, such interactions may further associate the experience of imitative correspondences within a prosocial context of positive arousal. To our knowledge, no research has yet examined how imitation becomes such a pervasively social phenomenon in childhood. However, as strong nativist views of imitative ability continue to be questioned, we must explore how an infant's social environment might facilitate the development of links between imitation and other experiences, including physiological and psychological states.

We hope that our reflections will encourage others to take an interest in the role of learning in the formation of flexible adaptive

social behaviours, and to further consider how such processes are influenced by universal developmental phenomena such as behavioural stereotypes.

Philosopher's disease and its antidote: Perspectives from prenatal behavior and contagious yawning and laughing

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Abstract: Accounts of behavior, including imitation, often suffer from *philosopher's disease*: the unnecessary, inappropriate, theoretically driven explanation of behavior in terms of cognition, rationality, and consciousness. Embryos are perversely unphilosophical and unpsychological, starting to move before they receive sensory input. Postnatal contagious yawning and laughing indicate that pseudo-imitative behavior can occur without conscious intent or other higher-order cognitive process.

When we seek to understand behavior—our own and that of others—we suffer from *philosopher's disease*: the unnecessary, inappropriate, theoretically driven casting of behavior in terms of higher-order cognitive processes. In these accounts, we often commit the *error of intentionality*, the over-estimate of our voluntary, conscious control of behavior. The antidote for philosopher's disease and its associated theoretical biases is research based on the natural priorities of organisms that is derived from objective descriptions of behavior. I suggest that we are not very good philosophers and can benefit from the examination of nontraditional sources for insight and guidance, especially prenatal behavior and postnatal contagious behaviors such as yawning and laughing (Provine 2012).

The best place to start the investigation of behavior is at the beginning—prenatal behavior. Early embryos are profoundly unphilosophical and unpsychological beings that start to move before they receive sensory input. They spond before they respond. Such motor precocity is an awkward fact for developmental psychologists who seek only environmentally driven causes of behavior (sensation/perception, learning, motivation, etc.) and neglect spontaneous movement (Provine 2012). The agenda of postnatal psychology fares poorly when forced upon the prenatal domain. Even after sensory input becomes available, it has little impact on most ongoing behavior during the prenatal period (Provine 1972). If this is not challenge enough, the spinal cord, not the brain, is the origin of the electrical discharges that drive much embryonic behavior (Provine & Rogers 1977). Both the functions and causes of embryonic behavior are novel and unique to the prenatal niche. Embryonic movement is essential for the development of joints, muscles, and the regulation of neuron numbers, behavioral consequences neglected by most developmental psychologists (Provine 2012). How many developmental psychologists know that paralyzing embryos blocks the naturally occurring death of motor neurons?

Instinctive yawning (Provine 2005), and laughing (2000; 2016; 2017) provide informative examples of erroneous thinking about the causes of behavior. Yawning is considered a pseudolinguistic gesture of sleepiness or boredom, and laughing is a play vocalization emitted in certain social settings, but neither is under strong voluntary control. We can neither convincingly yawn nor laugh on command, and attempts to do so seem fake and have long latencies (Provine 2012). However, lack of conscious control does not curtail the composition of fictive narratives to explain their occurrence.

Contagion provides another challenge to the myth of conscious control that is especially relevant to the issue of infant imitation of the sort reported by Meltzoff and Moore (1977) (Provine 1989a; 2012). When we yawn in response to observed yawns (Provine 1986) or laugh in response to observed laughs (Provine 1992), is it a conscious effort to imitate another person? Both options are unlikely, given the low level of voluntary control of yawning and laughing (Provine 2012). I suggest, instead, that such contagion is the involuntary consequence of activation of a feature detector for yawns or laughs in the observer's brain. The detector for laughter is probably acoustic—the sound of laughter triggers laughter of the listener (Provine 1992; 2000). The trigger for yawning is more broadly tuned—almost any stimulus associated with yawning will trigger yawns, including looking at them (Provine 1986; 1989b), hearing them, thinking about them (Provine 1986), or even reading about them as you are now doing (Provine 1986). If you desire a broader menu of contagious and pseudo-imitative acts, examine coughing, vocal crying, emotional tearing, reddening of the eyes, nausea/vomiting, and itching/scratching (Provine 2012).

Animal studies help clarify misunderstandings about neonatal imitation

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Abstract: Empirical studies are incompatible with the proposal that neonatal imitation is arousal driven or declining with age. Nonhuman primate studies reveal a functioning brain mirror system from birth, developmental continuity in imitation and later sociability, and the malleability of neonatal imitation, shaped by the early environment. A narrow focus on arousal effects and reflexes may grossly underestimate neonatal capacities.

Keven & Akins (K&A) propose that spontaneous aerodigestive behaviours may be mistaken for neonatal imitation; however, well-designed neonatal imitation studies already account for reflexive and arousal-driven responses (for a review, see Simpson et al. 2014a). When measuring arousal, either physiologically or behaviourally, and examining its relationship to imitative responding, evidence shows that for humans (e.g., Nagy et al. 2013) and nonhuman primates (NHP; e.g., Paukner et al. 2017; Simpson et al. 2014b), changes in arousal alone *cannot* account for neonatal imitation. In addition, K&A acknowledge that they “have not explained, so far, the differential responses of neonates

to specific gestures” (sect. 7.3.1, para. 2). We agree and further argue that differential imitation in neonates is incompatible with aerodigestive or arousal-driven explanations.

An additional misconception is that neonatal imitation is automatic and involuntary. Instead, infants exert active control over imitative responses and “provoke” previously imitated gestures, even after a delay, in both humans (Meltzoff & Moore 1994) and NHP (Paukner et al. 2011). Moreover, neonates are sensitive both to the type of action and the identity of the individual who modelled the action, initiating interactions only among social partners with whom they previously interacted (Paukner et al. 2011; Simpson et al. 2013). This ability is remarkable because it indicates that newborns are actively socially engaged (Meltzoff & Moore 1994). Consequently, delayed imitation is inconsistent with the proposal that neonatal imitation is a subcortical automatic response.

The aerodigestive hypothesis claims that imitative responses peak in the first week of life and decline in the following weeks. The data actually show the opposite for facial gestures: Neonatal imitative responses for tongue protrusion steadily increase in frequency from the first week to the ninth week (e.g., Oostenbroek et al. 2016; Meltzoff et al. in press 2017). Only after 3 months does the frequency of facial gesture imitation decline and infants begin to imitate other actions, such as sounds, vocalizations, and finger movements (Kuhl & Meltzoff 1996; Maratos 1998). Thus, although imitation does undergo changes with development, infants continue to reliably produce matching behaviours (for a review, see Simpson et al. 2014a). These findings support the idea that neonatal responses are not stereotypes but rather intentional, voluntary behaviours.

We agree with K&A that animal studies widen our understanding of various phenomena, including neonatal imitation. Nonetheless, in this instance, K&A neglect to consider animal studies in their potential to inform our understanding of infant social cognitive development (Gerson et al. 2016). For example, K&A claim, “neonatal imitation experiments provide the *only* evidence that mirror neurons are present at birth” (sect. 2, para. 7). Although we agree that neonatal imitation is behavioural evidence of a functioning mirror neuron system, this assertion overlooks NHP studies documenting cortical brain activity through electroencephalography (EEG) and reporting neural evidence of a mirroring system functioning from birth in newborn monkeys (Ferrari et al. 2012).

Furthermore, evidence from animal research is consistent with the premise that individual differences in neonatal imitation may reflect individual differences in sociability (Heimann 1989; Heimann et al. 1989). Neonatal imitation is hypothesized to be a developmental precursor for, and potentially predict, later social cognitive capacities (Heimann 1991; 2001; 2002; Suddendorf et al. 2013). Although this hypothesis has yet to be fully tested in humans, it has been tested in NHP (see recent review in Simpson et al. 2016). Infant monkeys who fail to exhibit neonatal imitation, compared to imitators, are less socially attentive (Simpson et al. 2014b), look less at faces in general and the eyes in particular (Paukner et al. 2014), exhibit poorer social cognitive skills such as imitation recognition (Simpson et al. 2015) and gaze following (Simpson et al. 2016), exhibit poorer goal-directed motor skills (Ferrari et al. 2009b), play less with peers and exhibit more anxious behaviour at one year of age (Kaburu et al. 2016). Together, these studies provide a more detailed view of the link between neonatal imitation, early social predispositions, and social development.

As a result of its plasticity, neonatal imitation may also be a fruitful target for intervention, as well as an early marker of sociality. Although we know little about the malleability of neonatal imitation in humans (Jacobson 1979; Kennedy-Costantini et al. 2016), animal studies enable the manipulation of infants’ environments and experiences. In monkeys, across both naturalistic and experimental settings, neonatal experiences impact infants’ social

capacities (Dettmer et al. 2016), including neonatal imitation, which is strengthened by face-to-face interactions in early infancy (Simpson et al. 2014a; Vanderwert et al. 2015). Contrary to the aerodigestive hypothesis, the aforementioned animal research strongly supports the social nature of neonatal imitation.

In sum, evidence to date is inconsistent with the view that neonatal imitation simply reflects spontaneous aerodigestive behaviours. Although we appreciate an approach mindful of the broader context of development, there is nonetheless a wealth of data that directly bear upon K&A’s arguments. A narrow focus on arousal effects and reflexes may grossly underestimate neonatal capacities. Recognizing such capacities and establishing neonatal measures of sociality may help identify neonates who fall outside the range of healthy social development and may increase opportunities to intervene and foster positive child outcomes.

An unsettled debate: Key empirical and theoretical questions are still open

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Abstract: Debates about neonatal imitation remain more open than Keven & Akins (K&A) imply. K&A do not recognize the primacy of the question concerning differential imitation and the links between experimental designs and more or less plausible theoretical assumptions. Moreover, they do not acknowledge previous theorizing on spontaneous behavior, the explanatory power of entrainment, and subtle connections with social cognition.

We praise the Keven & Akins (K&A) target article for emphasizing that neonatal imitation findings must be read in the broader context of sensorimotor development, especially as portrayed by Thelen (1979; 1981b). By describing tongue protrusion as one of many rhythmic stereotypies whose rate can increase in relation to arousal, and by indicating a precise timeline for the onset, development, and dropout of spontaneous tongue protrusion, K&A strengthen the arousal explanation of the neonatal imitation findings (Jones 2009). Nonetheless, their support for the arousal theory presents some shortcomings. Brief examination of some empirical studies and theoretical alternatives suggests that the debates about neonatal imitation, and its relevance to social cognition, remain more open than K&A imply.

K&A’s characterization of the operational definition of neonatal imitation (as “producing the modeled gesture more often than an unrelated one,” (sect. 2, para. 2) is imprecise. Most empirical studies of neonatal imitation operationalize imitation as greater frequency of a gesture in response to the same gesture than in response to other gestures. The operational definition entails reference to a plurality of gestures exhibiting the comparative increase just described. This point is of critical importance because Meltzoff and Moore (1977) were well aware that, if

only one gesture was matched, arousal would be the most plausible explanation, and they envisaged the operational definition of differential imitation precisely to exclude this explanation. Thus, the primary question is an empirical one: Is there evidence for differential imitation? If the answer is no, if only tongue protrusion matching is evidenced, then arousal is the most plausible hypothesis; if the answer is yes, the arousal explanation is no longer viable (Anisfeld 2005; Jones 2009; Meltzoff 2002; Ray & Heyes 2011).

In this regard, because current empirical literature remains ambiguous, K&A may be too hasty in siding with the negative answer. K&A do not mention a recent study providing evidence for differential imitation (Coulon et al. 2013); instead, they cite Oostenbroek et al. (2016), which did produce negative results but whose theoretical assumptions and experimental design are questionable. Relying on the supposition that early imitation has a major foundational role for social cognition and implies a strong motivation to imitate, Oostenbroek et al. (2016) averaged data across a large number of infants in their domestic environments, presenting 11 models one after the other. This design did not control variables potentially affecting infant behavior, introducing interference in the measurement of imitative responses (“delayed” imitative responses count as non-imitative because they occur when a different model is presented). A more realistic line of research takes each infant as its own control (e.g., Meltzoff & Moore 1992) and minimizes interference.

K&A’s examination of the theoretical alternatives is wanting in at least three aspects. First, explanations of differential imitation are not as narrow or impoverished as K&A suppose; some already rely on conceptions of the body schema formed through spontaneous prenatal behavior (Gallagher & Meltzoff 1996; Meltzoff 2009; Meltzoff & Moore 1997), including involvement of gustatory processes (Gallagher et al. 1998).

Second, a plausible account for differential imitation remains possible. An explanation of differential imitation does not have to postulate computational processes for the recognition of self-other similarities—which we agree is a major fault in Meltzoff and Moore’s (1997) account—nor does it have to postulate a module specifically evolved for imitation or related functions. In contrast, the commonalities between visual experiences and corresponding motor experiences may operate tacitly as the means by which spontaneous behaviors can be differentially induced (Vincini et al. 2017; Vincini & Jhang, revised and resubmitted). From this perspective, infants do not actively intend to match the behavior of others but, rather, tend to respond in a way that is more passively elicited. An implication of this perspective is that the more frequent an action is in spontaneous behavior, the easier it will be to induce it. Moreover, if early imitation is differential induction of spontaneous behavior, then it is inappropriate to use 11 control models (which entails provoking uneven levels of arousal). Rather, a small number of control models is sufficient to establish that specific models can induce their corresponding actions more than other models.

A third way in which K&A’s examination is wanting is that K&A reject a resonance or “entrainment” approach to differential imitation for debatable reasons. They delineate a model of “imitation without representation” (sect. 7.2 heading) that requires visual encodings of models to be matched with corresponding central pattern generators, and then they note that this systematic matching is a “tall order” (sect. 7.2, para. 7.2.1). In synchronization theory, entrainment requires participation of endogenously activated (“autonomous”) oscillations, whereas resonance can occur in a system that would not spontaneously oscillate by itself (Pikovsky et al. 2001). We therefore consider rhythmic stereotypies as a suitable basis for inducing differential imitation precisely because behaviors that are already active but not cognitively modulated are most susceptible to entrainment, and because distinct dynamic trajectories are the medium of oscillator coupling, not requiring mediation by recognition processes.

Finally, even if the arousal theory were correct, the link between infant arousal responses and social cognition should

not be dismissed altogether. A caregiver may respond to the infant’s spontaneous tongue protrusion with a facial expression, which in turn provokes arousal in the infant. In this way, the infant is drawn into an interaction—most readily, moreover, when the behaviors presented match and entrain spontaneous rhythmic stereotypies. Indeed, a caregiver may over-interpret the infant’s response as a social response, which promotes further interaction (Gallagher 2008). Therefore, a spontaneous behavior serving neurodevelopment for aerodigestive function may assume a new social-cognitive function—analogue to processes of recycling or reuse (Anderson 2016; Dehaene 2009).

In conclusion, we bring the question of differential imitation back to the foreground, and we discuss how it should be addressed empirically with the aim of developing a more plausible account. One should also consider previous theorizing on spontaneous behavior and explore the possible explanatory power of entrainment and subtler connections with social cognition. All this suggests that K&A’s discussion, although praiseworthy for its emphasis on rhythmic stereotypies, does not do justice to the complexity of the empirical and theoretical issues surrounding neonatal imitation.

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Ecological validity, embodiment, and killjoy explanations in developmental psychology

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Abstract: Keven & Akins (K&A) present a compelling alternative to the case for neonatal orofacial imitation, offered by Meltzoff and Moore. However, they provide little concerning what lessons their proposal has to offer developmental psychology more generally. I suggest three candidates and elaborate on how they raise outstanding methodological and philosophical questions for the approach taken in the target article.

Keven & Akins (K&A) proposal challenges decades of received wisdom concerning infant cognitive development. In addition, their case is important because it contains potentially significant methodological and philosophical lessons for cognitive science. Beyond a set of brief remarks concerning its relevance to nativist theorizing in developmental psychology, K&A leave us to guess what other lessons we ought to take away from their contribution. Below, I offer three partially related, but independent, proposals. First, their case suggests why a target behavior ought to be investigated in an ecologically valid way, especially before a hypothesis concerning its functional role has been formulated. Second, it demonstrates how attention to biology is not a peripheral side issue to explanations of psychological phenomena. Finally, their case highlights why alternative explanations, especially those that rely on simpler mechanisms to explain adaptive behavior, have to be ruled out prior to attributing cognitively sophisticated abilities to animals, including humans.

Meltzoff and Moore’s central goal was to show that infant imitative competence is present in neonatal infants (1977). In addition, they attempted to explain its presence through postulating

a cognitively sophisticated matching process (so-called “active intermodal matching” or AIM) that facilitates imitation via the recognition of the model as “like me” (Meltzoff & Moore 1995; 1997; Meltzoff 2007). However, their model presumes that the target behavior for analysis (i.e., TP/R) has been correctly identified as imitation behavior. K&A give us good reason to suspect it has not. Why not? One reason is that Meltzoff and Moore investigated TP/R independently of how human infant behavior is environmentally embedded. That is, they failed to attend to the conditions under which TP/R emerges, specifically under its typical pre- and postnatal environmental conditions. Without doing so, it is unclear how they could have properly formulated a hypothesis concerning the appropriate stimulus situation responsible for evoking TP/R. In other words, Meltzoff and Moore did not establish the ecological validity of their experimental design prior to attributing a functional role to TP/R. One of the central lessons from ethology is that, in order to correctly identify the biologically significant role of some behavior, it must be investigated under natural ecological conditions (see Tinbergen 1963). In my view, K&A’s case against Meltzoff and Moore depends on the notion of ecological validity, but it does so without an explicit discussion of the wider significance of this principle to developmental psychology. Without such a discussion, it remains unclear what broader implications ecological validity (as a methodological precept) has for the science of human cognitive development.

In addition to illustrating the danger of investigating behavior in an ecologically invalid manner, the K&A case against Meltzoff and Moore highlights the risk of attempting to explain the presence and structure of psychological processes in the absence of details concerning how those processes are embodied. Whereas it is true that Meltzoff and Moore (1997) have postulated a mechanism for imitation in infants, they treat it as if it could be investigated solely in psychological terms, that is, as if psychological explanation is autonomous from biological explanation. This view, articulated and defended by Jerry Fodor (1974; 1997), holds that psychology and biology are distinct domains of inquiry. This has been a staple of classical cognitive science, and seems to be a view shared by Meltzoff and Moore in practice, if not in principle. In contrast, one of the central claims of the embodied turn in cognitive science is that cognitive capacities are constituted by and “emerge from the recurrent sensorimotor patterns that enable action to be perceptually guided” (Varela et al. 1991, p. 173). This appears to be the context within which K&A’s hypothesis ought to be understood, and it looks unlikely that it could have been formulated if they, like Meltzoff and Moore, attempted to explain the presence of TP/R without considering how it unfolds through biological development. Although there is substantial disagreement among proponents of embodied cognitive science as to what its philosophical commitments are, or ought to be (see, e.g., Chemero 2011; Kiverstein & Clark 2009; Shapiro 2010) there is broad agreement that attention to bodily properties/processes is not dispensable or secondary to characterizing/explaining psychological phenomena. Do K&A agree that their case demonstrates why psychological explanation is not autonomous from biological explanation?

Finally, K&A’s hypothesis, if correct, is an example of how what was considered to be evidence of a high-level cognitive process (i.e., imitation) is, in fact, better explained through an appeal to so-called “low-level” mechanisms (i.e., rhythmically stereotyped motor behavior). This is analogous to what has been called a “killjoy explanation” in comparative psychology (Dennett 1983; Shettleworth 2010). Such an explanation is “killjoy” in the present context because it tempers the view that cognitively sophisticated mechanisms are required to explain human behavior. It is an appropriate description, here, because Meltzoff and Moore hypothesized that the arousal of TP/R behavior in infants is evidence of a complex cognitive process (i.e., AIM) that is then invoked to explain how infants solve a complex cognitive task (i.e., the correspondence problem). The issue is that if TP/R arousal is the result of the spontaneous activity of a subsystem

implicated in aerodigestive sensorimotor development, as K&A argue, then it does not require positing a cognitively sophisticated mechanism to explain. Are K&A committed to the view that developmental psychologists ought to consider killjoy explanations in problem areas other than imitation?

In conclusion, K&A’s hypothesis is important because it calls into question decades of theorizing predicated on the conclusion that neonatal infants possess cognitively sophisticated mechanisms for imitation. In addition, K&A’s hypothesis is significant even if it fails to completely account for the functional role of TP/R in development, because it shows how attention to biological details matters for the formulation and testing of hypotheses concerning the development of psychological phenomena. In any case, K&A’s hypothesis demonstrates how attributing functional significance to behavior is risky if done in an ecologically invalid way, without attention to how it unfolds as a result of embodied processes, and if a sophisticated cognitive mechanism is presumed to be responsible for its presence, when in fact it is not.

Authors’ Response

Beyond neonatal imitation: Aerodigestive stereotypes, speech development, and social interaction in the extended perinatal period

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Abstract: In our target article, we argued that the positive results of neonatal imitation are likely to be by-products of normal aerodigestive development. Our hypothesis elicited various responses on the role of social interaction in infancy, the methodological issues about imitation experiments, and the relation between the aerodigestive theory and the development of speech. Here we respond to the commentaries.

R1. Introduction

We would first like to thank all of the commentators for their insightful replies and the time spent to formulate them. As we looked through the commentaries, most of the topics raised fell into three (often overlapping) categories: The role of social interaction in the development of imitation, both in human and Old World primates more generally; the correct methodological constraints on past imitation experiments and on our own aerodigestive theory; and the relation between the aerodigestive theory and the development of speech. In writing our response, we first focussed on the origins of speech because it was central to many commentaries, and although it was the least developed subject in our article, this topic – the evolutionary and developmental origins of speech – best highlights how a detailed description of early mechanisms of respiration and ingestion can fit with other aspects of development such as the role of social interaction. We will thus start with the interaction between aerodigestive and speech

development (sects. 2.0–2.4) and then use this first section on speech to illustrate and bolster our responses to the two other general subjects of criticisms: methodological issues (sects. 3.0–3.5) and social interactivity (sects. 4.0–4.2).

R2. The origins of speech

Many of the commentators (Buck; Choi, Kandhadai, Danielson, Bruderer, & Werker [Choi et al.]; Mayer, Roewer-Despres, Stavness, & Gick [Mayer et al.]; Meltzoff; Murray, Sclafani, Rayson, De Pascalis, Bozicevic, & Ferrari [Murray et al.]) asked about the origins of speech and its relation to aerodigestive function. The aerodigestive theory has clear implications for the development of speech. According to our theory, the neonate does not arrive in the world with a set of innate, multimodal, cortical representations. Instead, neonatal behaviour begins with subcortical oscillators for repetitive behaviours, orofacial and otherwise – behaviours initiated and driven by arousal mechanisms. By birth, the stereotypies of aerodigestion have been woven together into the first sensorimotor sequences of the human body. These motor runs – for example, breathing, swallowing, peristaltic motions of the tongue and esophagus – are themselves periodic events, controlled by networks of oscillators and tempered, even *in utero*, by multimodal sensory feedback. There are no cortical motor commands prior to birth, no feedforward predictive encodings that await confirmation or error signals. Nor are the patterns of somatosensory feedback that occur as a natural result of these oscillatory motor sequences represented *qua* the predictive “results” of a given motor “command.” Instead, as motor learning progresses, ever more complex, multimodal feedback is integrated into these oscillatory networks, a process that yields systems that are responsive in real time to the vicissitudes of a dual system for eating and breathing. Somehow, from this unlikely starting point, speech begins – and our commentators have rightly expressed curiosity about this bootstrapping process or outright doubt that this is possible.

R2.1. What are the evolutionary origins of human speech?

It seems clear that, in the target article, the authors have stumbled into a robust discourse about the evolutionary origins of speech. Mayer et al. provide comprehensive analyses with evidence that “there are at least some core speech movements which are direct ontogenetic adaptations of preexisting digestive movements.” A different, though structurally similar proposal for the ontogenetic adaptation of speech from pre-existing movements can be found in the work of Ghazanfar et al. (2012), derived from MacNeilage’s view (Borjon et al. 2016; Chandrasekaran et al. 2009; Ghazanfar et al. 2012; Shepherd et al. 2012), that speech has evolved from rhythmic facial expressions to which vocalizations have been added. Murray et al. emphasize that these mouth movements were long ago co-opted into early infant-parent dynamic interaction.

Although we are not experts on the evolution of speech, a few things seem clear. Our aerodigestive theory is not meant to be an evolutionary theory of *speech* but, rather, is meant to explain why neonatal imitation is unlikely to occur given the facts of aerodigestive development.

However, our theory is compatible with both sides of this debate, with the evolution of speech from either fetal aerodigestive behaviours or orofacial behaviours such as yawning, blinking, scowling, smiling, and so on. (Dai & Hata 2006; Kanenishi et al. 2013; Kurjak et al. 2007; Sato et al. 2014; Yigiter & Kavak 2006).

In our target article, we concentrated on aerodigestive behaviours in the belief that TP/R fits neatly into the class of aerodigestive behaviours. Apart from the neonatal imitation literature, and unlike lip-smacking among New World Primates, there is little to suggest that TP/R is a universal, affiliative human behaviour (cf. Murray et al.). That said, facial expressions of the fetus and neonate have a developmental trajectory that is parallel to aerodigestive development, that is, from individual stereotypies to sensorimotor sequences. In a set of experiments, Reissland et al. (Reissland et al. 2011; Reissland et al. 2012; 2013) showed that from 24 to 36 weeks gestational age (GA) these individual action units begin to coalesce into “Gestalts” of emotional expressions, such as a “happy face” or a “cry face.” Prior to 24 weeks, single-action units predominate facial expressions, whereas by 36 weeks, 85% of action units co-occur with two to four other units. Just as aerodigestive stereotypies coalesce into motor runs by 36 weeks GA, coherent facial expressions emerge over the same time period. Moreover, just as suckling and respiration are “practiced” *in utero* without, for example, air to breathe, the “pain face” of a fetus at 36 weeks GA occurs spontaneously and independently of any (visible) harmful event. So, aerodigestive behaviours and facial expressions share the same developmental trajectory. Thus, our theory is consistent with *either or both* evolutionary theories.

R2.2. Is the aerodigestive development consistent with early, pre-linguistic behaviour of the infant?

We know that prior to speech acquisition, infants younger than 4 months of age begin to vocalize. Therefore, according to our view, infants must be able to learn such behaviours prior to gaining cortical control of articulatory structures. Meltzoff argues that infants younger than 4 months “produce diverse cooing sounds, which require tongue movements markedly different from suckling and tongue stereotypies.” Consequently, if “infants cannot control their tongues prior to 4 months of age” and “all tongue movements are purported to be the stereotypic thrust/retraction involved in suckling,” then the aerodigestive theory must be false.

Our claim is that orofacial stereotypies develop via “practice” prior to birth and are then incorporated into complex, sensorimotor sequences through networks of interacting oscillators. Both *learning* and tongue *control* occur before and after birth, the result of the developing oscillatory networks in the brainstem. Importantly, tongue thrust is a primitive *reflex*, not a stereotypy, a difference that makes a difference. Unlike primitive reflexes, infant stereotypies are highly variable – for example, small or large (just over the lip line or far beyond it) and in all directions (to the right or the left, or straight down the midline). In our view, stereotypies that continue to occur alone, independently of sensorimotor runs, organize cortical motor space through the somatosensory and proprioceptive feedback from the full range of possible movement.

Accordingly, TP/R explores the deformation space of tongue movement, across the full range of protrusive tongue movements. This variation provides a bridge between aerodigestive and articulatory behaviours. For example, **Mayer et al.** suggest that tongue-bracing contacts during swallowing are a subset of the tongue-bracing contacts in speech. Stated differently, the motor activation space of tongue-brace during swallowing falls primarily within the activation space of tongue-brace for speech. If tongue-brace is a stereotypy – and it is – this transition is not mysterious. The stereotypy has already explored the sensorimotor space of tongue-brace prior to speech learning. Note that we are not claiming that Mayer et al.’s view is necessarily true. Our claim is that sensorimotor learning occurs subcortically in early human development; therefore, some articulatory movements need not require cortical input to be learned. Which tongue movements require cortical input depends upon the *type* of tongue movement. Ballistic movements such as catching a drip of ice cream as it escapes from the cone probably require cortical input to learn or initiate such directed tongue movements. This is our claim in the target article.

R2.3. How might human speech develop out of neonatal stereotypies?

Neither of us is a specialist in language development, but the commentators’ questions (cf. **Choi et al.**, **Murray et al.**) sparked our interest in the recent literature on speech development and oscillatory entrainment. If perinatal behaviour is a function of subcortical networks of central pattern generators (CPGs), and if mature speech also involves repetitive, rhythmic movements, then perhaps interaction between parents and infants form coupled systems of oscillators; that is, parental speech entrains the pre-linguistic behaviour of infants. Perhaps the best example of this research project is found in the work of Ghazanfar et al., who characterized human speech as an inherently multimodal capacity that has evolved from facial expressions/stereotypies (i.e., the MacNeilage view; see Borjon et al. 2016; Chandrasekaran et al. 2009; Ghazanfar et al. 2012; Shepherd et al. 2012). Their experiments suggest that at least three types of pre-linguistic learning can be explained in terms of coupled oscillation modulated by speaker and listener arousal, namely cooperative vocal adjustment at a distance, the maturation of turn-taking, and the development of the “phee” call in infant marmosets. Several of these experimental results are directly applicable to the human case.

First, human infants might learn conversational turn-taking in much the same way as infant marmosets. Ghazanfar et al. (2008) reported that infant marmosets, during the first postnatal days, respond to recordings of their own voices and parental cries with the same frequency of response and response time. This suggests the inability of the infant to distinguish between its own voice and the voices of others. By 2 months of age, infant marmosets attained the adult temporal pattern of vocal turn-taking, with ever decreasing response time to the parental voice. The authors explain this reduction in terms of the vocal entrainment of the infant’s call by the parent. In the human case, the dorsal cochlear nucleus receives somatosensory feedback from the face and parts of the vocal

tract, thus a rudimentary mechanism to identify one’s own vocalizations. Auditory stimulation with vocal tract and facial proprioceptive feedback is “my voice,” auditory stimulation without feedback equals “someone else’s voice.” Once a human infant differentiates her own voice from another speaker’s, auditory entrainment can begin.

Second, self-entrainment might explain the importance of infant cooing. Cooing, the production of vowel-like sounds, involves large facial movements – the pursing of lips (“oo”), a wide-open jaw (“ah”), lip retraction (“ee”), and so on. Such expressions are not unknown to the infant. Many of these expressions can be mapped directly onto the stereotypies that comprise the newborn’s behavioural repertoire or fall within the variations seen in the first stages of stereotypy acquisition. Fagan (2014) reported that infants deaf from birth make less frequent vocalizations of all kinds. After early cochlear implantation, they resumed a normal pattern of pre-linguistic vocalizing. However, deaf newborns did not resume normal rates of crying and other vocal signals of distress. Fagan concludes that infant cooing/babbling “are primarily motivated by auditory feedback.” To put this slightly differently, the infant’s own vocalizations might create a self-sustaining training-cycle – of vocal production followed by both auditory and somatosensory encodings. As long as arousal by self-vocalization is speech sound specific, that is, causes the vocalization of multiple “vowels,” learning paired associations between somatosensory (S1) and auditory (A1) encodings will occur. This suggestion may explain why 4-month-old infants cannot judge auditory-visual mismatches when prevented from making articulatory movements. As long as the categorization of *speech sounds* is primarily somatosensory – or if somatosensory categorization is required to entrain speech production – an infant will not be able to classify phonemes or differentiate between them without self-production. Nor would an infant be able to learn a new phoneme without first trying to reproduce it and thus see *what it feels like*.

Third, entrainment may explain the development of audiovisual matching between the voice and lip movement of a speaker with the lips, the capacity that underlies the McGurk effect (Chandrasekaran et al. 2011). The 2-month-old infants look longer at matches between facial movements and speech sounds (Patterson & Werker 2003); at 4 months, infants reverse this correlation, paying more attention to *mismatches* (Kuhl & Meltzoff 1984). Intuitively, this looks like an initial period of multimodal learning followed by the ability to perceive exceptions based upon learned audiovisual associations. In speech, the motion of the lips and the resultant auditory signal are both rhythmic events with the same periods of oscillation, synchronized in space and time. Thus, temporally synchronized auditory and visual signals, matched in periodicity, indicate a common source/speaker of these signals. But from where does this visual information about dynamic faces come? We know that A1 and its adjacent areas contain a high percentage of multimodal (audiovisual) cells in adult primates. But at birth, the visual system has yet to begin processing dynamic patterns of visual stimuli, a necessary requirement for training up A1 cells that associate facial movements and their respective sounds. In the superior colliculus, the alignment of audiovisual maps is also experience dependent and will not occur until about 4 months of age.

One plausible route for this association is by way of the pulvinar, a division of the thalamus. In adult primates, human and otherwise, dynamic facial expressions are matched to speech through input from the middle temporal (MT) visual area in the posterior bank of the superior temporal sulcus (STS) (Ghazanfar et al. 2008). If cortical vision developed hierarchically, one would expect area MT to lag behind visual area 1 (V1) in maturity. But directional sensitivity arises in V1 and MT *at the same time*, around postnatal 4–7 weeks. The key here may lie in the pulvinar (Kaas 2015). Newborn primates have a *transient* pathway from retina to pulvinar and then from pulvinar to visual associative area STS including area MT (Warner et al. 2012). So visual motion information via the pulvinar could be critical to the formation of multimodal, audiovisual cells in auditory cortex. The timing here is highly suggestive. If direction selectivity begins by 4–7 weeks, infants in the Patterson and Werker study (2003) would have had, on average, a few weeks of associative training and thus the basis for preferential looking.

R3. Methodological issues and assumptions

R3.1. The cross-target methodology: Should we trust it?

Several commentators argue that neonatal imitation can still be a viable theory when a wider array of data is taken into account (Meltzoff; Simpson, Maylott, Heimann, Subiaul, Paukner, Suomi, & Ferrari [Simpson et al.]; Vincini, Jhang, Buder, & Gallagher [Vincini et al.]). This evidence comes largely from experiments designed to test neonatal imitation using a methodology that has changed very little after the first-wave improvements. When an experimental methodology continues to produce a tangle of positive and negative results over a 35-year period, this is deeply worrisome. It suggests that the methodology is somehow flawed and that its continued use will not produce definitive results in the future. Witness here the competing results of two recent, careful studies by Oostenbroek et al. (2016) and Simpson et al. (2014a).

In the target article, we attempted to set this issue aside in order to develop a positive theory. But ours is not a theory of how or why neonatal imitation occurs: It is meant to *explain away* the positive results of neonatal imitation experiments, not to vindicate them. As the commentators demonstrate, we must address some issues of procedure and statistical analysis in the neonatal imitation work. Given the constraints of space we will mention one example that has relation to the aerodigestive mechanisms.

A standard part of the cross-target methodology is the “burst-pause procedure” that in Meltzoff and Moore (1989, p. 955) was justified as follows: “In previous work with newborns it was reported that attention and responsivity were maximized if adult gesturing was alternated with an interval in which the adult remained passive ...” (Meltzoff & Moore 1983). If we look back at Meltzoff and Moore (1983, p. 707), the authors reported that: “We found in preliminary work that a constant demonstration of the target gesture was not maximally effective in eliciting imitation. Therefore, in our design the experimenter alternated between the presentation of the gesture and a passive face. We are not certain why our burst-pause procedure is the more powerful, but we can suggest three possibilities.” The three possibilities then given were that (a) it

gave infants several periods of time over which to organize their motor response; (b) the burst-pause paradigm nicely “bookended” the demonstrated gesture, thereby accentuating what was to be imitated; or (c) the paradigm mimicked the give and take of conversational turn-taking, thus encouraging infant response. All of these options assume that imitation occurs and that the question about this methodology is *why it increases imitation*.

The right question to ask is *why* the new methodology changes infant behaviour and whether those factors are related to imitation or to extraneous factors. For example, it could be that in addition to increasing attention, the methodology also increases arousal. Or perhaps the methodology increases negative affect and thus responsiveness. In the still-face-effect experiment, an adult who stares without facial expression or movement causes anxiety in infants as measured by fussing or crying, increased heart rate, skin conductance, and vagal tone (Bertin & Striano 2006; Ham & Tronick 2006; Moore & Calkins 2004; Striano 2004). This effect begins in infants between 1 and 1.5 months of age (Bertin & Striano 2006; Bigelow & Power 2012), just around the age of testing (Meltzoff & Moore 1992; 1994). Yet imitation experiments use what amounts to a still face stimulus as a control condition. We now also know that neonates prefer their mother’s face to that of a stranger (Bartrip et al. 2001) and to prefer a new face over a previously viewed face or a noncommunicative face (Cecchini et al. 2011). So multiple aspects of the burst-pause paradigm are linked to negative affect.

Finally, as we saw from the research on marmoset turn-taking, the third option may well have hit the nail on the head. Six-week-old infants may already have learned turn-taking behaviour through interaction with their parents, what amounts to a “call-and-response” sequence in which behaviour is inhibited during the “call” and the inhibition is released when the static gesture ends, thus producing *more* gestures thereafter. But this need not involve imitation *per se*, merely a move towards conversational turn-taking or a reflexive “wait and listen/see” disposition that reduces noise while in the listening phase. Because the authors assumed that the burst-pause paradigm increased *imitation*, they did not investigate any hypotheses about *why* “attention and responsivity were maximized” by the new paradigm. In our opinion, it is time to go back and look carefully at the assumptions incorporated into the cross-target paradigm.

R3.2. If your explanation is in terms of arousal, what explains the differential response?

As a number of our commentators have pointed out, the primary empirical question is not whether arousal increases the production of infant stereotypies, that is, the base rate of production, but whether there is evidence for a differential response – more mouth opening (MO) in response to modeled MO, not TP; more TP in response to TP, not MO (Meltzoff, Simpson et al., Vincini et al.). As Simpson et al. assert, “differential imitation in neonates is incompatible with aerodigestive or arousal-driven explanations.” Moreover, the search for differential responses should not focus on TP alone, given that one needs to show a pattern of differential responses across neonatal behaviours.

Let's take the easiest question first, why we have focused primarily on TP. We do think the case of TP/R is special. It is the only gesture that has consistently garnered more positive than negative results in imitation experiments for which there is no ready, alternative explanation. In fact, TP/R is the most commonly modelled gesture across studies; approximately 85% of studies investigating imitation in neonates up to 6 weeks of age have included this gesture (Oostenbroek et al. 2013). Many reports of a differential response to other gestures have failed on replication, even in Meltzoff and Moore's own experiments (i.e., MO in the 1994 experiments). Moreover, TP/R is the standard comparison condition for the imitation of mouth opening, another gesture often cited as known to elicit imitation. So, if TP/R is not imitated, then a large and convincing body of evidence for the existence of neonatal imitation vanishes. All things being equal, such a result would probably spell the end of the neonatal imitation (NI) research project. A vindication of the TP/R results, in contrast, would require the further investigation of differential responses to other gestures.

That said, our central worry about the criterion of differential imitation concerns the comparison class and the statistical analysis of the cross-target experiments. As **Kennedy-Costantini, Oostenbroek, Suddendorf, Nielsen, Redshaw, Davis, Clark, & Slaughter (Kennedy-Costantini et al.)** point out in their commentary, a recent longitudinal study of neonatal imitation at ages 1, 3, 6, and 9 weeks (Oostenbroek et al. 2016) reported that "(infants) were just as likely to produce the gestures in response to control models as they were to matching models" (p. 1334). By looking at a limited, cross-section of the data, the Oostenbroek researchers were able to reproduce the same positive effects as reported in earlier studies. They concluded that failure to include adequate control conditions or test infants across multiple time points in previous studies has resulted in the false impression that infants selectively copy tongue protrusions, thereby perpetuating the idea that newborn imitation exists. For our part, given that we see the "gestures" of infants as neonatal stereotypies, this makes a good deal of sense. Because we can actually categorize and then count up the kinds of neonatal stereotypies, just as Thelen did (Thelen 1981b), we have the right comparison class in hand. So, at least for neonates, the question cannot be "tongue protrusion or mouth-opening." This doesn't represent the statistical landscape. Of course, no one knows whether these results will themselves stand the test of time. But one possibility—the one on which we are betting—is that there will be no positive results at all. Hence, no explanation will be needed.

If we are wrong, and the positive results prove robust, then we must give an alternative explanation. At present, we do not have a single reason, but we do have several we think are worth pursuing. For example, there is the intriguing result in Meltzoff and Moore (1992) that MO duration is longer than TP duration. When the authors tested MO using a dynamic stimulus, MO duration increased; it was twice as long on average than when the static stimulus was used. However, a dynamic presentation of TP produced only slightly more frequent TPs than in response to the static display (which were not timed only for duration). This difference in response suggests that

the causal mechanisms of MO and TP differ. Therein could lie a tale of how arousal could differentially affect the rate and duration of TP and MO: Perhaps arousal/apprehension inhibits MO and increases TP. At this point in time, we have no clear explanation of *why* this should occur. But note that arousal plays a crucial role in Ghazanfar's examples of speech development as well, both in how infant marmosets learn to adjust the intensity of their voices as a function of listener distance (Choi et al. 2015) and in how parental calls, timed to infant vocalization, produce mature "phee" calls in the infant over time (Ghazanfar & Zhang 2016). These events occur beyond the neonatal period, of course, so they are only illustrative of how the context of arousal differentiates its causal effects.

We have also wondered whether Anisfeld (1996) and others might be right in their explanation that the higher rate of MO in the mouth opening condition, compared to its rate in the tongue protrusion condition, may be explained as a by-product of infants' TP/R responses. TP/R and MO/C co-vary with each other: Increase in one results in a decrease in the other. Given that overall level of oral activity stays roughly constant in the two conditions, the rise in the rate of TP/R in the tongue protrusion condition seems to reduce the rate of MO/C in this condition. The higher rate of MO in the mouth opening condition compared to its rate in the tongue protrusion condition may then be on account of the lowering of the MO/C rate in the tongue protrusion condition, not to its raising in the mouth opening condition. For instance, in Meltzoff and Moore (1983) the rates of MO/C and TP/R are about the same in the mouth opening condition, whereas the rate of TP/R is substantially higher than the rate of MO/C in the tongue protrusion condition. So what may rise and fall under different conditions is actually the rate of TP/R. More generally, we worry that even neonatal arousal is not a homogeneous state. Here the presupposition is that increasing arousal is like turning up the speed dial on an oscillating fan: It makes everything go faster. But there is no reason why this should be so, that the effects of arousal should be undifferentiated. Why, exactly, given the complexity of the neonatal brain, *must* this be so?

R3.3. Is our argument for the aerodigestive theory a form of Occam's razor?

Several commentators argue that we should apply Occam's razor to decide between the imitation and aerodigestive theories (**Beisert, Zmyj, & Daum [Beisert et al.]; Jones**). Originally, Occam's razor was the dictum that we ought not to multiply explanatory entities beyond those needed. As the old medical dictum goes: If you see hoofprints, look for horses not unicorns. Certainly part of our argument has followed Occam's razor understood in this way. We know that subcortical oscillators control the central aerodigestive behaviours of early infancy; neurodevelopmental research also suggests that the maps of primary visual cortex, S1 and M1, are still highly immature at birth. So, taken together, if infants respond differentially to modelled tongue protrusion with more frequent tongue protrusions (than to other gestures), we ought not to look for the complex

representational structures required by the hypothesis of opaque imitation: that is, visual representations of facial gestures, somatosensory patterns of self-produced facial gestures, cortical motor commands that produce TP, plus the various mechanisms of mapping and association that yield genuine imitation. There is no independent evidence for the existence of such structures or abilities. Consequently, we should train our attention on the kinds of processes that we know to exist – or think are likely to exist – at birth in human infants. This would be an argument of the classic form.

Still, when dealing with the massive complexity of the human brain – and here we include the neonatal brain as well – we rarely have conclusive facts in hand of the sort that would support a simple version of Occam's razor. Instead, what we suggest is more akin to inference to the best explanation than Occam's razor. The question is this: What if we were to stand back from the specific and highly contested results of neonatal imitation experiments and look instead at the distance traveled over 35 years of neurodevelopmental research, in psychophysics, neurophysiology, and neuroanatomy. What picture emerges? We know that neural mitosis and migration begins via chemical cues and/or via the use of nearby cells for pathfinding; we also know that prior to environmental input, Ca²⁺ activity influences every aspect of neural development from cell mitosis, migration, arborization, transmitter expression, axonal growth – and that once transducers are in place and functioning, development will continue based upon patterned environmental stimulation. We also know that this process of neural scaffolding can involve “two steps forwards, one step back” – the expression and re-expression of transmitters, the growth of temporary structures such as the subcortical plate, and of transient neural pathways, connection areas that will disappear when no longer needed. Although this developmental process proceeds simultaneously in multiple systems, by birth the human cortex is still immature. The alternating columns in V1 that segregated visual input by eye have yet to form, an essential organizational structure for stereoscopic vision. Although the subcortical motor system is well developed at birth, the cerebrospinal system has yet to establish functional connections between M1 and the spinal gray matter, a process that will require protracted development after birth.

It is this cumulative picture that seems at odds with the existence of the infrastructure, at birth, required for cross-modal or amodal information transfer. Whether one supposes that such structures are innate or learned, the results of genetic transcription or neural activity, there is no reason to think that the neonatal brains “comes with” such resources. It is also at odds with the kind of intentional explanations of neonatal behaviour often given by researchers. There is no *recognition* that your gesture is like mine, or *probing* a model to reveal model identity (Meltzoff & Moore 2002) or *understanding* that you are a thing “like me” (Meltzoff 2007). So, either we “deflate” what is normally meant by, for example, a motor command (for there are no motor commands in the cerebrospinal system of the neonate), or we look towards the kinds of mechanisms that we know to exist. We then ask how the neonatal brain bridges the seemingly vast gap between non-intentional and intentional cognitive processes. **Zappettini** asks whether we, the authors, are fond of

deflationary or “killjoy” accounts, of accounts that take *prima facie* cognitive tasks and explain them in non-cognitive terms. We deny that we have a predilection for killjoy accounts. We are not killjoys by nature. Rather, we agree with **Booth, Beisert et al.**, and **Provine** that we should avoid cognitively rich interpretations when there are more plausible cognitively lean interpretations available.

R3.4. Is neonatal imitation connected to later social skills?

Simpson et al. argue that neonatal imitation is connected to later social skills. If there is a connection between neonatal imitation and later social skills, first and foremost there should be a connection with the later imitation skills. However, many studies failed to find a connection between neonatal imitation and later imitation (Abravanel & Sigafos 1984; Fontaine 1984; Heimann et al. 1989; Jacobson 1979; Kugiumutzakis 1999). On the contrary, neonatal imitation drops out after 3 months only to reappear after 6 months. Among researchers who accept neonatal imitation as a fact, it is controversial whether this “drop-out” is significant. Does the imitation of tongue-protrusion simply end abruptly at 2–3 months? Or does the infant merely move on to other forms of interaction with adults and resume a different repertoire of imitative behaviors a few months later? This is Meltzoff and Moore's (1992) explanation of the phenomenon of “drop-out.”

As we have shown in the target article, that mammalian aerodigestion develops in two phases: (1) from the onset of isolated orofacial movements *in utero* to the postnatal mastery of suckling at 3 months after birth; and (2) thereafter, from preparation to the mastery of mastication and deglutition of solid foods. This division in the maturation of the mammalian aerodigestive system has important consequences for the question of neonate imitation drop-out. Suppose, now, that tongue protrusion *qua* spontaneous neonatal behaviour itself ends between 2 and 3 months after birth. And suppose it does so *because* the developmental phase of which it is but one part comes to an end as a whole. This fact would suggest that the “imitation” of tongue protrusion does not end because the infant loses interest in copying orofacial gestures, but because spontaneous tongue protrusion itself declines as this first phase of aerodigestive maturation draws to a close. This fact – that an aerodigestive developmental stage, involving a period of spontaneous tongue protrusion, coincides with the period during which neonates “imitate” tongue protrusion – is highly significant. This coincident phase makes it more plausible that the increase in neonate tongue protrusion in the experimental setting is the result of some extraneous cause – for example, general arousal in the face of an interesting stimulus. Proof of an independent but coincident developmental phase, then, again raises the spectre that we have mistaken a spontaneous behaviour for an imitative one.

R3.5. Given that your theory posits a dynamical system of aerodigestive CPGs, why did you dismiss imitation via entrainment in the target article? What about mirror neurons?

One of the central features of the cross-target methodology is the alternation of each static display of gesture modeling

with a period of static neutral face during which the response of the infant is recorded. During both periods, the model works to minimize any differences in presentation, paying particular attention to inadvertent social signals that might cue the production of stereotypies and/or create experimental artefacts. The experiment seems almost perfectly designed to *preclude* the dynamic entrainment of the infant's behaviour by the model's behaviour. There is no entrainment without oscillatory activity and oscillatory activity is conspicuously absent from the standard cross-target methodology. This is why, in the target article, we dismissed entrainment as an explanation of the reported NI results.

In retrospect, a more nuanced answer is possible. There is one stage in the static cross-target paradigm that is dynamic, namely at the temporal boundary between the presentation of the static gesture and the model's transition to the static face: for example, when retraction of the tongue marks the completion of static TP modeling or after one full period of TP/R oscillation. Whether this has any effect on the neonate's behaviour is an open question. But entrainment theory could explain *why* the burst-pause methodology seems to promote imitation as well as why the imitative effects of gesture modelling are so weak (because there is only one very slow period of oscillation). That said, confirming a dynamical theory of behavioural entrainment would require a quite different experimental setup, one that uses dynamic stimuli and records neonatal behaviour concomitantly.

As to mirror neurons, we agree entirely with **Fitch's** commentary. Were it not for the discovery of neonatal imitation in macaques, it would have been hard to explain why adult macaques, a species notoriously lacking in robust imitative behaviour, had mirror neurons at all. So neonatal imitation in macaques has served to bolster claims that mirror neurons underlie imitative behaviours in primates more generally. We do not wish to deny the existence of mirror neurons. But we are sceptical of any claim that mirror neurons explain the NI experimental results or that mirror neurons must be present in neonatal macaques/humans *because* of the NI experimental results. Independent evidence of either claim is needed before proceeding down that explanatory path. Still, contra **Leisman**, it is hard to imagine that mirror neurons exist in the human neonate. Mirror neurons require a functional, mirror neuron network. If active intermodal matching (AIM) is unlikely to be true given the immaturity of the neonatal human cortex, then the same arguments apply to the cortical network/s required to drive mirror neurons – and thus to the existence of mirror neurons in the perinatal period.

R4. Social engagement and infant automatons

R4.1. Social engagement

A number of our commentators have stressed the importance of social interaction for infant development (**Aitken**; **Buck**; **Desseilles**; **Libertus**, **Libertus**, **Einspieler**, & **Marschik** [**Libertus et al.**]; **Murray et al.**; **Simpson et al.**). We are entirely in agreement with this view and, more generally, with the interactive nature of human infants. At birth, infants come into the world entirely dependent upon the caretaking of adults. Infant survival requires the constant attention of their caregivers.

This makes care as important to human infants as normal physiological development, for example, of a functioning aerodigestive system at birth. But looking beyond bare survival, the extended period of postnatal motor development has the consequence that *what* is learned during this period rests heavily on parental interaction.

Parents (or caregivers) facilitate the lion's share of the infant's interaction with the world prior to the attainment of goal-oriented action. For the neonate, being carried, cuddled, changed, fed, bathed, bounced, and generally responded to “in words or deed” are the rich events that foster immediate infant learning. Moreover, this learning involves multiple dimensions, the social and emotional no less than learning within the standard sensory and motor domains. Infants learn to be soothed by touch and voice, “read” the prosody of human speech and the emotional “temperature” of their social environments, to make eye contact and visually explore a human face, distinguish between the friend and “foe” (the still-face effect), and to relish in human interaction. Last, but not least, they learn how to *engage* their caregivers – or, as my (Akins) mother-in-law used to say, “how to run a household from the cradle.” The inert, non-interactive infant is an infant at risk. But such infants will also learn far less about the world in general and about human social relations (cf. **Casartelli & Parma**).

Infant-maternal¹ bonding is thus essential for normal development. In the target article, we mentioned the multitude of ways in which this occurs (see sect. 7.3). These processes arise in the neonate alone (e.g., the olfactory recognition of the mother's colostrum at birth), the mother alone (e.g., oxytocin release, increased sensitivity to the infant's cry), and through interaction between the two (e.g., kangaroo care, the coordination of mother and infant heartbeat). Social interaction begins immediately at birth – turning towards the mother's voice, visually exploring her face, making facial expressions such as smiles or grimaces – and gradually grows more sophisticated. We suggest that this interaction “works” – creates and maintains a bond – at least in part because of the automatic human propensity for intentional interpretation. We see in that now-famous, first Pixar video, two lamps (one a large anglepoise lamp and the other a small gooseneck) interacting *as* a mother and child. They play, are watchful, talk, remonstrate, and even sulk, cycling through the gamut of parent-child interactions. Indeed, we cannot help but see them as persons despite knowing that lamps cannot have intentional states (or have children for that matter).

Our interactions with the newborn are no less intentionally infused; we see, and cannot help but see, the crying, grimacing, and smiling of a human infant as *actions*. This is not an argument that we think infants are vegetative automatons, as **Aitken** would have us say. Rather, in practical terms, our own propensity to see intentional states is so deeply engrained that we see intentional behaviour even when our perceptions conflict with what we know. For example, we see the neonate smiling even though we know that the transition to the social smile takes ~8 weeks after birth to develop. Add infant-adult turn-taking to the mix once the infant can distinguish self- from other- produced voices – that is, remaining silent/inactive when the mother acts/speaks and then continuing activity when the mother stops – and any infant becomes entrancing to his or her caregivers (or at least to those disposed

to be entranced at the outset). The net result of this and other such processes is maternal bonding, a state essential to the infant in all respects. In other words, the interactive baby has little need for a complex capacity for imitation. Nor is this possible, as **Campos and Neito** say, “their perceptive and attentional capacities (Volpe 2008), and face processing and intersensory processing abilities (Bahrick et al. 2004; Johnson et al. 2015; Lewkowicz 2014; Morton & Johnson 1991), among others, are too weak yet.” The infant who reacts, in whatever way, to our attention reaps the benefits that advocates of neonatal imitation so often invoke.

R4.2. Infants as automatons

A related misconception of our view is that we are throwbacks to the bad old days of psychological behaviorism. Or worse, that we see infants as automatons that exhibit reflexive behaviours without variation or learning. To quote **Aitken** (who quotes Polani & MacKeith [1960]), we are tainted with the view that “the newborn infant may be described as a tonic animal with oropharyngeal automatisms and neurovegetative mechanisms.” This is *not* our view although we would be hard pressed to say exactly what it is like to be a neonate. One misconception concerns our talk of stereotypes, a term we have adopted from the literature and which distinguishes between neonatal reflexes and stereotypes. Few sensorimotor neuroscientists talk in terms of reflexes anymore, at least not in the classical Sherrington sense, except for the patellar reflex arc in children and adults. Indeed, neonatal “reflexes” are notoriously difficult to evoke, requiring an experienced clinician.

In any event, neonatal stereotypes are not invariant or “released” by specific stimuli. On the contrary, our suggestion is that so-called neonatal stereotypes are useful precisely because they are *not* invariant. Precipitated by general arousal, their constant variation serves to explore the full -range of sensorimotor space, and, as **O’Sullivan and Caldwell** point out, the stereotypic actions are likely to play a significant role in the development of associations between sensory and motor representations of the same behaviour. Infant stereotypes occur precisely when the somatosensory and motor cortices are developing functional connections within and between the M1 and S1 regions, as well as developing the functionality of the corticospinal tract. Of course, it is an essential part of our view that proprioceptive and motor learning begins *in utero*. But in just the way that “suckling” *in utero* is a faint facsimile of actual suckling after birth, sensorimotor activity *in utero* fails to replicate the physics (and freedom) of terrestrial locomotion after birth. It’s a whole new ballgame, as they say, once on land. So, for this reason, it is not a bad idea to “wire” the sensorimotor system “in place,” at least for any species with a large and complex sensorimotor repertoire. At least, *a priori*, that would seem to be the case.

R5. Conclusion

The aerodigestive theory is built upon wide-ranging experimental results, from the neurophysiology of mammalian aerodigestive, sensory, and motor systems, the practices of pediatric clinical neurology, the neurochemistry of

activity-dependent neural processes, and developmental psychology more generally. It situates the gestures at issue within a known class of fetal/infant behaviours, rhythmic movements, but also within the known processes of early neural development. In contrast, after 40 years of investigation, the putative mechanisms of neonatal imitation remain oddly disconnected from the disciplines of human development. From where we stand, at least, the onus is now on the proponents to explain where this system of imitation resides and how it functions.

NOTE

1. Bonding can occur with any caregiver, of course. Indeed, men can “learn” to lactate but are sidestepping the issue of what forms of bonding are possible, by concentrating on newborn-maternal bonding.

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[The letters “a” and “r” before author’s initials stand for target article and response references respectively.]

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