



PAPER

Learning to imitate individual finger movements by the human neonate

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Abstract

Imitation in human neonates, unlike imitation in young infants, is still regarded as controversial. Four studies with 203 newborns are presented to examine the imitation of index finger, two- and three-finger movements in human neonates. Results found differential imitations of all three modelled gestures, a left-handed pattern, and a rapid learning mechanism. The lateralized behavioural pattern suggests the involvement of a right lateralized neural network, and the mechanisms described in this study – (i) the accurate imitation of all aspects of the model's movements, (ii) the rapid learning component, and the (iii) the early sensitive period might fulfil the criteria for filial imprinting.

Research highlights

- Human neonates imitate the extension of one-, two- and three-finger movements
- Imitations were characterized by a lateralized left-handed pattern
- A rapid learning mechanism was identified
- Based on the analysis of the literature a sensitive period is indicated
- Potential imprinting mechanisms are suggested to subserve neonatal imitation.

Introduction

A series of studies (Meltzoff & Moore, 1977, 1983; Field, Woodson, Greenberg & Cohen, 1982; Abranavel & Sigafos, 1984; Kugiumutzakis, 1985; Reissland, 1988; Heimann, Nelson & Schaller, 1989) have reported that newborn infants as young as a few hours old imitate the movements that they see others performing. These reports on neonates imitating the previously seen movements of others, particularly those they cannot visually observe on themselves (such as facial actions) were,

however, incompatible with the Piagetian model of early cognitive development that projected the appearance of such abilities only around the 10th–12th month of life (Piaget, 1962). Despite the findings, neonatal imitation has remained a controversial ‘fuzzy phenomenon’ (Heimann, 2001) that several studies failed to replicate (Hayes & Watson, 1981; McKenzie & Over, 1983; Anisfeld, Turkewitz, Rose, Rosenberg, Sheiber, Couturier-Fagan, Ger & Sommer, 2001), and reported the phenomenon as lacking the evidence (Jones, 2009).

Among those with positive results were a study from rural Nepal involving newborns in the first hour of life, with the umbilical cord still attached (Reissland, 1988), reports from well-controlled and designed experiments (Heimann *et al.*, 1989; Meltzoff & Moore, 1983), studies with interactive design (Kugiumutzakis, 1985; Nagy & Molnar, 2004), and with an ethological, statistical approach (Nagy, Compagne, Orvos, Pal, Molnar, Janszky, Loveland & Bardos, 2005). These studies are so varied that methodological differences can hardly account for the negative results of others. Yet the negative results may still provide important information on neonatal imitation. Anisfeld *et al.* (2001), for example, when comparing the imitation of the two most commonly examined gestures – tongue protrusion and

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mouth opening – found evidence only for the imitation of tongue protrusion gestures. The two gestures, however, are not independent, as later neurophysiological research confirmed. Microstimulation of neurons responsible for opening the jaw in the face primary motor area (MI) evokes additional tongue protrusion in 64% of the neurons (Yao, Yamamura, Narita, Martin, Murray & Sessle, 2002). Eliciting mouth opening may elicit tongue protrusion; therefore even if neonates do imitate mouth opening, an additional tongue protrusion could co-occur and confound the results. Jones proposed an alternative explanation (Jones, 2006). When she played music, 4-week-old infants increased the frequency of their tongue protrusion in the silent period, after the music was over; therefore she proposed that tongue protrusion is an oro-facial exploratory response to interesting stimuli. The existence of such a mechanism, however, does not exclude the possibility that newborn infants also imitate these gestures when it is modelled to them. What these studies suggest is that the administration of multiple oro-facial gestures in the same experiment might fail to result in differential response if the movements are co-regulated on a neurophysiological level.

Previous research suggests that imitation in young infants is a motivated behaviour (Nagy & Molnar, 2004) that is best elicited in a communicative paradigm (Bard, 2007). Newborns were found not only to imitate but also to spontaneously reproduce previously imitated gestures while apparently waiting for the experimenter's response (Nagy & Molnar, 2004). Newborn infants, therefore, are not only capable of responding to a model's movement by imitating it, but they also have the capacity to initiate and sustain an interaction. We speculated a hypothetical model of human imprinting as a possible underlying phenomenon (Nagy & Molnar, 1994, 2004), but the model has not been investigated further.

Our study examined the imitation of three non-facial gestures, specifically the raising of one, two and three fingers in a large sample of neonates. Besides this design avoiding multiple oro-facial gestures, a further advantage of the fine-motor finger movements was their relatively low baseline frequency, and therefore changes in the movement are easier to detect. It was even suggested that such intentional, individual finger movements appear only in the second half of the first year when motor pathways become sufficiently myelinated (Eyre, Miller, Clowry, Conway & Watts, 2000). Our earlier study (Nagy *et al.*, 2005) reported the imitation of one finger (the index finger) raising gesture in 39 newborns using a statistically based analysis of all the movements the babies made. Study 1 aimed to replicate the existence of the index finger raising imitation in the perinatal period

with a large sample of newborns, and as such, to provide much-needed confirmation of the existence of the neonatal imitation. For a more accurate description of the nature of the changes, not only the frequencies but also the durations of the movements were analysed.

If imitation is interpreted broadly as a communicative act, in theory any response by the newborn that is temporally related to the stimulus could be treated as a response to the model (Kugiumutzakis, 1999; Bard, 2007). Babies may respond in a variety of ways, for example, such as suddenly becoming still as a sign of increased attention. They could look in the direction of the experimenter's face or hand, they could move body parts, such as legs, feet, toes, turn the head, and respond more specifically, moving their arms, the entire hand, and their fingers. Finger movements can also vary: one finger, two fingers can move, more fingers could spread, extended, half-extended. The movement can be lateralized or bilateral, or may become lateralized gradually over time. Movements can be lateralized with reference to the baby's own body (left, right or bilateral, regardless of the experimenter's movements), specular (i.e. mirroring the experimenter), or anatomic imitations (e.g. left finger movement as a response to a left finger movement of the model). Imitative responses, however, regardless of whether they are communicative or not, must match the stimuli shown by the model. The study therefore measured all arm and different finger movement patterns made by the baby (Table 1). The significant advantage of this method is that no rules and decisions were made on the function and the meaning of the baby's movement, on what counts as a 'response' to the model, and on the length of the response time. All arm and finger movements made by the baby were analysed both at baseline and in the experimental periods regardless of the intention of the baby. We predicted that if newborns have a tendency to match the experimenter's movement, they would selectively increase the frequency and duration of the index finger movement when an index finger extension gesture was modelled, and would selectively increase the frequency and duration of the raising of the two fingers when the two-finger movement was modelled, and raising the three fingers when the three-finger movement was modelled (Studies 2 and 3). The outcome numbers would not represent an absolute indicator that describes how well individual babies imitate, but this ethological-based coding provides a statistical approach to detect imitation. In order to further ensure that the results were not due to an unknown order-effect, Study 4 was planned and the finger movements were modelled in randomized orders.

We further predicted that the pattern of the imitative responses offers insight into the underlying mechanisms.

Table 1 Coding system for arm and finger movements

Behaviour	Code	Definition
Baby arm movements	Arm movements	Code used to indicate all arm movements: vertical, horizontal, outwards, or in front of baby.
Baby finger movements	Inaccurate index finger	Index finger moves out of line along with other fingers – tip of finger past knuckles of other fingers but does not extend fully
	Accurate index finger	Index finger fully extended, with clear gap from the rest of fingers
	Two fingers	The index and the third fingers extended, partially or fully, with clear gap between them and rest of fingers
Experimenter	Three fingers	First two fingers and thumb extended, partially or fully with clear gap between them and rest of fingers
		One-finger movement
		Two-finger movement
		Three-finger movement

Our earlier study (Nagy *et al.*, 2005) found that newborns imitated more with their left than their right hands. The study, however, was not designed to test the laterality of the imitative gestures; thus the results must be treated with caution. Study 1 therefore further aimed to examine the laterality of the neonatal imitation by randomly allocating newborns into conditions where the experimenters showed only left, or right, or left and right finger movements throughout the experiment. If the behavioural appearance of imitation was found to be lateralized, such a result may allow us to speculate on a potentially lateralized neural network underlying neonatal imitation.

Study 1a: Imitation of index finger movement

Method

Participants

Data from 133 newborns (72 boys, 61 girls) were collected, 75 born with vaginal delivery, 58 with caesarean section.

The average weight was 3334 g (range: 2170–4350, $SD = 459.89$), the average gestational age was 38.75 weeks (range: 36–42, $SD = 1.36$) and the mean age of the babies was 2.11 days ($SD = 1.87$, 0–6 days) at the time of the examination. Between 2004 and 2007, at the time of the data collection for this experiment, the prevalence of caesarean section was an average of 39% at the Department of Obstetrics and Gynecology at the Albert Szent-Gyorgyi Medical University at the site of the data collection. The prevalence rate of caesarean section among the participants in this experiment is therefore in line with the prevalence of caesarean section deliveries in the clinic.

Although only babies in alert, quiet condition were examined, data of 12 newborns had to be excluded from

the analysis because the experimental phase had to be terminated within less than 180 seconds due to fussiness, or the newborn falling asleep or due to an incomplete dataset. Data of 121 newborns were included in the analysis. All mothers gave their written informed consent, and the studies were approved by the Ethical Committees of the Albert Szent-Gyorgyi Medical University and the University of Dundee.

Procedure: experimental setting

Babies were examined in a separate room of the neonatal ward under constant illumination and ambient temperature (28°C). Newborns were examined approximately 30–90 minutes after feeding, an optimal time for an awake, alert, quiet state. Infants were placed in an infant seat, on their backs in an upright, comfortable position, with their heads turned towards the video camera and the experimenter. The hands of the experimenter were directly seen from the same camera angle.

The procedure was similar to procedures used in naturalistic studies (Kugiumutzakis, 1980, 1985; Reissland, 1988) with neonates, showing the strongest resemblance to the procedure described by Kaye and Marcus (1978) with 6-month-old infants. In the baseline period ‘for the first 2 min (less if the infant verged on crying), the experimenter engaged in normal, flexible interaction and vocalization’, wrote Kaye and Marcus (1978, p. 144). Then ‘Whenever the infant’s eyes met his [experimenter’s], he immediately made a series of five open-and-close mouth movements’, and ‘Every time the infant’s gaze left the experimenter’s eyes and returned’, ‘he repeated the model’; ‘the timing of his behaviour was controlled by the infant’s eye movements’. ‘Trials continued so long as the infant cooperated’, ‘which took 9.3 min’ (Kaye and Marcus, 1978, p. 144). In our experiment the modelling and responses continued as long as the infant cooperated. This relatively prolonged experimental period employed in Study 1 allowed us to

record and thereafter measure the changing pattern of the responses, that is, whether finger movements indeed increasingly matched the model's over time.

Baseline period (BP). The experiment started with a 2-minute baseline period, when the experimenter presented a natural face and interaction, but did not show any of the finger gestures to the babies.

Experimental period (EP). Study 1a aimed to confirm the imitation of index finger movement gesture. Study 1b, using a subset of the participants from Study 1a, examined whether newborns adapt their imitative responses to the model's movement to two-finger and three-finger imitative gestures. Studies 1a and 1b are reported separately because of the differing sample size.

From the moment the experimenter showed the first gesture, the experimental period started, lasting for an average of 474 seconds ($SD = 214.60$) and the experimenter modelled the movement of raising the index finger to the newborn. This length is comparable to the one described by Kaye and Marcus (1978). The mean number of gestures by the experimenter was 5.17 per minute, depending on the baby's attention ($SD = 2.36$). The administration of the gestures was a 'burst-like' presentation when the baby was looking in the experimenter's direction, that is, a series of dynamically presented index finger raising gestures with an approximately 2-second/gesture speed (similar to that described by Meltzoff and Moore (1983) and Kaye and Marcus (1978)). After the gesture was presented, the baby's response period began. After the babies' response (incomplete or complete finger movements), the experimenter showed another gesture. If the baby did not respond, the experimenter waited for approximately 30 seconds and continued with the presentation of the next gesture.

Conditions. In order to avoid any lateral bias by the experimenter or the experimental setup, infants had been randomly allocated into one of the following three groups: one-third (30.6%, $n = 37$) of the infants in the Left group, where the experimenter modelled the finger movements only with her left hand, a further one-third (35.5%, $n = 43$) of the infants were allocated to the Right group, where the experimenter modelled the finger movements only with her right hand, and one-third (33.9%, $n = 41$) of the infants were in the Both group, where the experimenter modelled the finger movements randomly with her left and right hands throughout the experiment.

Equipment. A Panasonic NVGS27B digital video camera was used to record the experiments. The videotapes

were digitized and edited for analysis using Ulead-VideoStudio 8 software. The Observer Pro 5 system was used for frame-by-frame coding of the data, and Observer XT 9.0 to extract the basic statistics from the codings, both frequency and duration based measures.

Coding. A descriptive, statistical-based approach was used. This means that all movements, regardless of whether they were imitative or not, were coded both in the baseline and in the experimental periods. No judgements were made about the function and the intention of the movements. This approach was taken in order to completely eliminate the subjective elements from the coding and offered an objective, statistical way to examine the existence of neonatal imitation. We assumed that the increase in the targeted movements in the experimental period would be statistically detectable without the need for subjective judgements.

The states of the babies were also coded using the behavioural states of the newborn as described by Prechtl (1974). Variables 'sleepy', 'drowsy', 'awake', 'aroused' and 'crying' were continuously coded. The baseline period and the subsequent experimental periods were coded frame-by-frame for each baby. The same coding system has been used in all studies (see Table 1).

Three independent coders coded the data. None of the coders were involved in the data collection, the analysis or the design of the studies. Twenty-five percent of the data (that is, every fourth video) were double coded (by coders A-B, A-C, and B-C) for reliability. The reliabilities were averaged, and the first coder's coding was included in the data set. Cohen's kappas for inter-rater reliabilities of frequency in the baseline period ranged from .60 to .81 with an average of .70, while for duration data ranged from .66 to .93 with an average of .78. Cohen's kappas for frequencies in the one-finger imitation stage ranged from .61 to .82 with an average of .70, while for duration data ranged from .62 to .92 with an average of .76.

Statistical analysis. Frequency (movement/minute) and duration variables were calculated by the Observer system and used for statistical analysis. Mixed design Multivariate Analysis of Variances (MANOVAs) were conducted to investigate the effect of the experimental period (Stages: Baseline versus Experimental) and Laterality Condition (Left, Right, Both) on the change of the frequencies and the duration of the different movements on the left, right and both sides. SPSS 15.0 for Windows statistical software (SPSS, Inc., Chicago, IL) was used, and $p < .05$ was accepted as significant throughout.

Results

Frequency of the movements

Complete index finger movements. Inspection of the data showed that 16.5% of the babies had decreased, 2.5% had no change in, and 81% had increased frequency of complete index finger movements between the baseline and experimental stages.

In a mixed design analysis, the frequencies of the index finger movements, incomplete index finger movements, arm movements, two-finger and three-finger movements were compared in the baseline and the experimental periods across the three conditions, when they were presented with the left, right or both hands of the experimenter. A 2 (Stage: Baseline/Experimental) * 3 (Demonstration Condition: Left/Right/Both) MANOVA on the frequencies (newborn movement/minute) of the left, right and both index finger movements revealed a significant main effect of *Stage*, $F(3, 116) = 15.13$, $p < .001$, $\eta_p^2 = .28$, but no significant *Stage*Condition* interaction, $F(6, 234) = .30$, *ns*.

Post-hoc univariate analyses showed that babies significantly increased the frequencies of both the left (Mean BP = 0.62, $SE = 0.09$, Mean EP = 1.29, $SE = 0.13$, $p < .001$) and the right (Mean BP = 0.65, $SD = 0.08$, Mean EP = 1.18, $SE = 0.11$, $p < .001$) index finger movements, and the frequencies of the 'both' index finger movements (Mean BP = 0.03, $SE = 0.01$, Mean EP = 0.07, $SE = 0.02$, $p = .02$).

Incomplete index finger movements. Inspection of the data showed that 40.5% of the babies decreased, 0.8% had no change in, and 58.7% increased the frequency of incomplete index finger movements between the baseline and the experimental stages.

There was a significant main effect of *Stage*, $F(3, 116) = 4.63$, $p = .01$, $\eta_p^2 = .11$, in the frequencies of the incomplete index finger movements, but no *Stage*Condition* interaction $F(6, 234) = 1.10$, *ns*.

Both the frequencies of the left (Mean BP = 1.99, $SE = 0.17$, Mean EP = 2.82, $SE = 0.26$, $p = .001$) and the right (Mean BP = 2.08, $SD = 0.18$, Mean EP = 2.76, $SE = 0.24$, $p = .001$) incomplete index finger movements increased, but not the both movements (Mean BP = 0.91, $SE = 0.13$, Mean EP = 0.91, $SE = 0.09$, *ns*) (see Figure 1A).

Other movements. Arm movements: A 2 (Stage: Baseline/Experimental) * 3 (Demonstration Condition: Left/Right/Both) ANOVA revealed a significant main effect of *Stage*, $F(3, 116) = 5.84$, $p = .001$, $\eta_p^2 = .13$, but no *Stage*Condition* interaction, $F(6, 234) = .35$, *ns*.

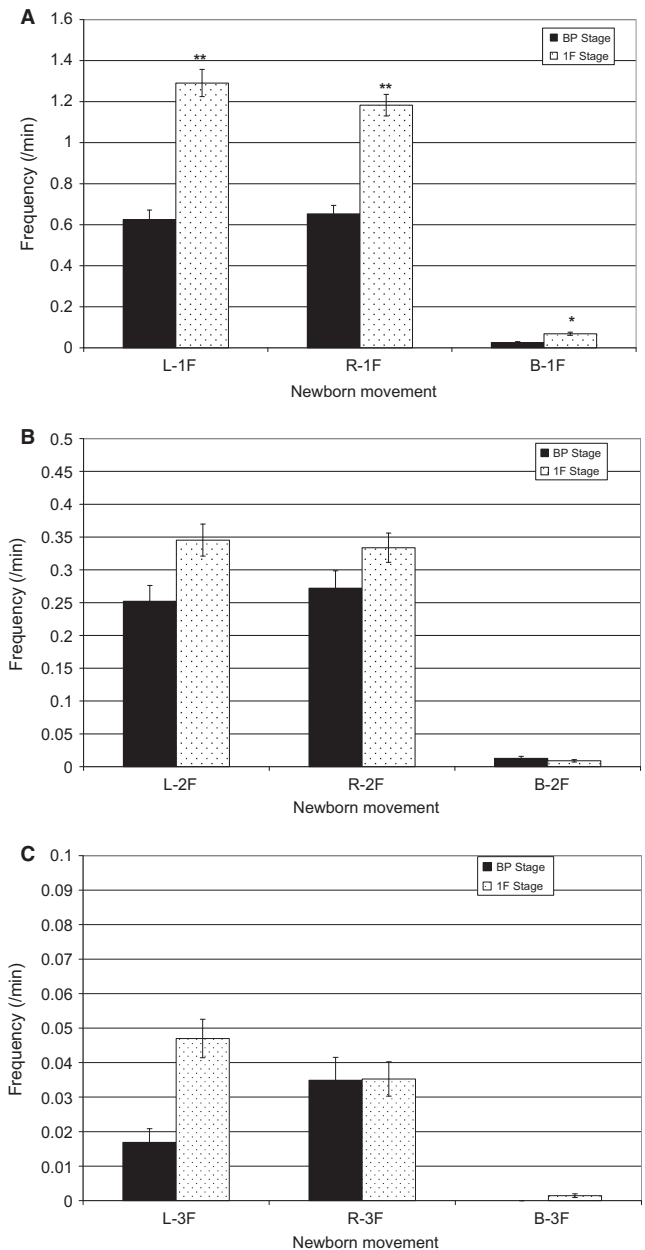


Figure 1 Study 1a. A, B and C: Frequency of index extension response (right or left) after left, right and both 1-Finger (Figure A), 2-Finger (Figure B) and 3-Finger (Figure C) extension model. ** $p < .01$; * $p < .05$.

There was no main effect of *Stage*, $F(3, 116) = 1.72$, *ns*, and no *Stage*Condition* interaction, $F(3, 234) = 1.01$, *ns*, for the frequencies of the two-finger movements, and similarly, there was no main effect of *Stage*, $F(3, 116) = 2.15$, *ns*, and a significant tendency for *Stage*Condition* interaction, $F(3, 234) = 2.13$, $p = .05$, $\eta_p^2 = .05$, for the frequencies of the left, both but not the right three-finger movements in the 1F Stage (see Figures 1 B and C).

Duration of the movements

See Supplementary Information 1.

The change over time

Increasing accuracy across the first five cycles. In order to further examine the temporal unfolding of the finger movements, the first five imitative cycles have been analysed. The number of *cycles* started by the experimenter by modelling, followed by any response by the baby until the emergence of the baby's first inaccurate and accurate index finger raising movements was also recorded.

Comparing the rank orders (cycles 1 to 5) of the occurrence of the first inaccurate and accurate finger movements showed that babies produced their first accurate index finger raising movement about two cycles later than their first inaccurate index finger extension movement, $t(2, 235) = 3.30, p = .001$ (Figure 2).

Left movements occur earlier. During the EP, left-sided accurate index finger raising movements occurred about two cycles earlier compared to the right-sided first accurate index finger extension movements (Left = 4.09 cycles, $SD = 3.78$, Right = 5.86 cycles, $SD = 5.86, t(2, 120) = -2.05, p = .04$).

Left hand advantage. Average handedness scores were computed for the first five complete and first five incomplete and complete index finger movements in the baseline and experimental periods. Left (labelled 1) and right sided movements (labelled 2) were averaged, resulting in a handedness score for BP and EP, complete and incomplete index finger movements. The closer the value is to 1, the score represents more left handed and fewer right handed movements. Results showed signifi-

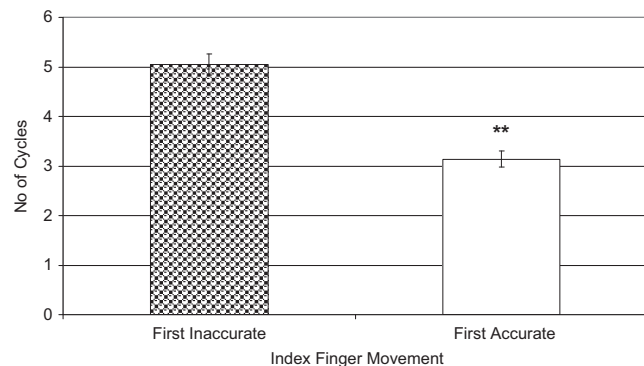


Figure 2 Study 1. The first occurrence of the inaccurate and accurate index finger imitations.

(Inaccurate = 5.05, *s.e.m.* ± 0.022, Inaccurate index finger movement = 3.14, *s.e.m.* ± 0.16, Accurate index finger movement = 0.39, *s.e.m.* ± 0.023) ** $p < .01$.

cantly more left-handed movement (inaccurate + accurate index finger movements) in the experimental period compared to the baseline, $F(1, 59) = 5.03, p = .03, \eta_p^2 = .08$ (BP = 1.55, $SE = .03$, EP = 1.47, $SE = .03, p = .03$). Such a right-to-left shift originated from the increased frequency of the left accurate index finger movements in the experimental period (BP = 1.54, $SD = .32$, EP = 1.49, $SD = .32, Z = -1.98, p = .048$).

In summary, babies increased the frequency of target movements during the experimental period (see Figure 3A), suggesting that they selectively matched the experimenter's movements assuming that the increase of the arm movements in the EP is unrelated to the increase of the index finger extension gesture. In addition, they responded faster with their left hands and became more accurate with time, as if the responses unfolded through inaccurate trials towards an accurate matching the experimenter.

Study 1b: Imitation of two- and three-finger gestures

Materials and Methods

Participants

Study 1b aimed to examine the existence of two- and three-finger imitations. Eighty-eight babies completed Study 1b Stage 'two-finger', and of those, 69 babies completed Study 1b Stage 'three-finger'. Data of the 69 babies who completed both stages of Study 1b were included in this analysis (40 boys, 29 girls, 39 born with vaginal delivery, 30 with caesarean section). In the two-finger stage, 31 babies were modelled by left, 31 babies by right and 26 babies by 'both', left, right hands randomly. In the 'three-finger' stage the numbers were 27, 26 and 16, respectively.

Their average weight was 3419 g (range: 2170–4350, $SD = 471.39$), the average gestational age was 38.84 weeks (range: 36–41, $SD = 1.33$), the mean age of the babies was 2.06 days, ($SD = 1.67, 0-6$ days) at the time of the examination.

Procedures

The experimental setting, equipment, coding, statistical analysis were identical to those in Study 1a. Movement frequencies per minute were compared to those observed in the baseline of Study 1a.

Experimental period. Newborns were first (Study 1b, Stage 'two-finger') modelled two-finger movements



Figure 3 (A) Imitation of the index finger raising movement; (B) Imitation of two-finger raising movement; (C) Imitation of three-finger raising gesture.

(raising the second and third finger, as if forming a 'V'), and then they were shown three-finger gestures (Study 1b, Stage 'three-finger', thumb, first and second fingers extended simultaneously), with methods similar to Study 1. The average duration of the two-finger imitation session was 171.51 seconds ($SD = 99.51$), and the three-finger imitation period was 145.75 seconds ($SD = 109.22$).

The mean frequency of the experimenter's movements was 6.38/minute ($SD = 2.87$) in the two-finger imitation period, and 6.06/minute ($SD = 3.14$) in the three-finger imitation period.

Three independent coders coded the data and 25% of the data (that is, every fourth video) were double coded (by coders A-B, A-C, and B-C) for reliability. The reliabilities were averaged, and the first coder's coding

was included in the data set. Cohen's kappas for frequencies in the two-finger period ranged from .63 to .91, with an average of .73, while for duration data ranged from .74 to .95, with an average of .83. Cohen's kappas for frequencies in the three-finger imitation stage ranged from .60 to .91, with an average of .73, while for duration data ranged from .64 to .95, with an average of .83.

Results

Frequency data

Frequency of the two-finger movements. Inspection of the data showed that 27.5% of the babies decreased, 5.8% had no change in, and 66.7% increased the frequency of

two-finger movements between the two-finger and three-finger stages.

In the analysis, the frequencies of the two-finger and three-finger movements, the index finger movements, incomplete index finger movements, and arm movements were compared at baseline and in the experimental period.

A MANOVA with two levels of *Stage* ('two-finger'/'three-finger') on the frequency (newborn movement/minute) of the left, right and both two-finger movements found a significant main effect of *Stage*, $F(3, 66) = 5.16, p = .003, \eta_p^2 = .19$, that is more two-finger movements in the 'two-finger' than in the 'three-finger' stages. Post-hoc univariate analyses showed that the frequencies of both the left (Mean 'Two-finger' Stage = 1.03, $SE = 0.11$, Mean 'Three-finger' Stage = 0.58, $SE = 0.09, p = .001$) and the right (Mean 'Two-finger' Stage = 1.00, $SE = 0.14$, Mean 'Three-finger' Stage = 0.66, $SE = 0.09, p = .007$) two-finger movements were higher in the 'two-finger' compared to the 'three-finger' stages (see Figure 4A).

Frequency of the three-finger movements. Inspection of the data showed that 14.5% of the babies decreased, 20.3% had no change in, and 65.2% increased the frequency of three-finger movements between the three-finger and two-finger stages.

A MANOVA with two levels of *Stage* ('two-finger'/'three-finger') on the frequency (newborn movement/minute) of the left, right and both three-finger movements found a significant main effect of *Stage*, $F(3, 66) = 3.80, p = .01, \eta_p^2 = .15$, that is more three-finger movements in the '3-finger' than in the 'two-finger' stages. Post-hoc univariate analyses showed that the frequencies of the left (Mean 'Two-finger' Stage = 0.09, $SE = 0.03$, Mean 'Three-finger' Stage = 0.34, $SE = 0.06, p < .001$), right (Mean 'Two-finger' Stage = 0.08, $SE = 0.03$, Mean 'Three-finger' Stage = 0.34, $SE = 0.06, p < .001$) and both (Mean 'Two-finger' Stage = 0.004, $SE = 0.004$, Mean 'Three-finger' Stage = 0.12, $SE = 0.03, p = .002$) three-finger movements were higher in the 'three-finger' compared to the 'two-finger' stages (see Figure 4B).

Frequency of the other movements. The frequencies (newborn movement/minute) of the left, right and both arm movements ($F(3, 66) = 0.97, n.s.$), the incomplete finger movements, $F(3, 66) = 1.34, n.s.$, and the complete finger movements, $F(3, 66) = 0.55, n.s.$, were not different between the 'two-finger' and the 'three-finger' stages.

Duration data

See Supplementary Information 2.

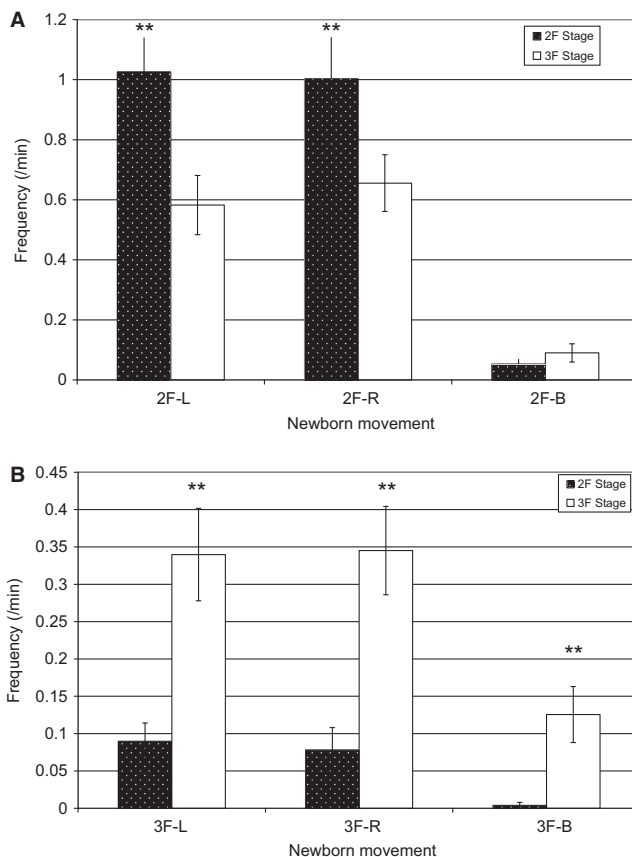


Figure 4 Study 1b. A and B: Frequency of 2-Finger response (left, right or both, Figure A) and the 3-Finger (left, right or both, Figure B) movements after the 2-Finger and the 3-Finger extension model. ** $p < .01$; * $p < .05$.

Study 2: Imitation of the three-, then two-finger movements

In order to ensure that the results were not due to an order-effect, to control for the order, 20 newborns were tested with the modelled movements in reverse order, that is, with these babies, three-finger movements were modelled first, followed by the two-finger modelling (see Figures 3B and C).

Method

Participants

Twenty-three babies were recruited for Study 2 (15 girls, 8 boys, 10 born with vaginal delivery, 13 with caesarean section). Data of 22 babies were codable. Their average weight was 3255 g (range: 2720–4650, $SD = 520.11$), the average gestational age was 38.69 weeks (range: 37–41,

$SD = 1.11$), and the mean age of the babies was 1.73 days, ($SD = 1.25$, 0–5 days) at the time of the examination.

Procedures

The experimental setting, equipment, coding and statistical analysis were identical to those in Studies 1a and b. The experiment started with the baseline period followed by the three-finger and the two-finger stages. All babies were randomly presented the finger movements with the left and the right hands of the experimenter.

Experimental period. Newborns first were modelled three-finger movements (thumb, index and middle fingers) and then the two-finger (index and middle fingers) movements, randomly with the left and right hands of the experimenter. The average duration of the three-finger imitation stage was 395.07 seconds ($SD = 157.16$), and the two-finger imitation period was 353.65 seconds ($SD = 149.30$). The mean frequency of the experimenter's movements was 4.37/minute ($SD = 1.31$) in the three-finger imitation stage, and 5.63/minute ($SD = 2.36$) in the two-finger imitation period.

Two independent coders coded the data and 15% of the data were reliability coded between the coders. Reliabilities were averaged and the first coder's coding was included in the dataset. Cohen's kappas for the frequencies in the baseline period ranged from .78 to .91, with an average of .83, while for duration data ranged from .95 to .99, with an average of .96. Cohen's kappas for frequencies in the two-finger imitation stage ranged from .79 to .88, with an average of .85, while for duration data ranged from .87 to .97, with an average of .94, and Cohen's kappas for frequencies in the three-finger imitation stage ranged from .87 to .96, with an average of .91, while for duration data ranged from .93 to .98, with an average of .96.

Results

Frequency of the movements

Two-finger movements. Inspection of the data showed that 27.3% of the babies decreased and 72.7% of the babies increased the frequency of two-finger movements from the baseline to the two-finger stages.

In the analysis, the frequencies of the two-finger, three-finger, index finger movements, incomplete index finger movements and arm movements were compared in the baseline, two-finger and three-finger stages.

Comparing the frequencies (newborn movement/minute) of two-finger movements in the three stages (Stages: Baseline/Three-Finger/Two-Finger) there was a significant main effect of *Stage*, $F(2, 42) = 3.14$, $p = .04$, $\eta_p^2 = .15$. Post-hoc comparisons adjusted according to Fisher's LSD method showed that babies significantly increased the frequencies of the two-finger movements in the two-finger modelling stage compared to when three-finger movements were modelled (Mean 2F = 1.42, $SE = 0.31$, Mean 3F = 0.72, $SE = 0.16$, $p = .02$) and the frequencies of the two-finger movements were marginally more frequent in the two-finger, compared to the baseline stages (Mean 2F = 1.42, $SE = 0.31$, Mean BP = 0.83, $SE = 0.24$, $p = .06$) (see Table 2). The frequencies of the two-finger movements were not significantly different between the baseline and the three-finger stages.

Three-finger movements

Inspection of the data showed that 4.5% of the babies decreased, 36.4% had no change in, and 59.1% of the babies increased the frequency of three-finger movements from the baseline to the three-finger stages.

Comparing the frequencies (newborn movement/minute) of the three-finger movements in the three stages (Stages: Baseline/Three-Finger/Two-Finger) there was a significant main effect of *Stage*, $F(2, 42) = 4.15$, $p = .02$, $\eta_p^2 = .17$. Post-hoc comparisons with Fisher's LSD adjustment showed that babies significantly increased the frequencies of the three-finger movements in the three-finger modelling stage compared to when two-finger movements were modelled (Mean 3F = 0.42, $SE = 0.18$, Mean 2F = 0.05, $SE = 0.02$, $p = .05$) and the frequencies of the three-finger movements were higher in the three-finger, compared to the BP stages (Mean 3F = 0.42, $SE = 0.18$, Mean BP = 0.04, $SE = 0.04$, $p = .05$) (see Table 2). The frequencies of the three-finger movements were not significantly different between the BP and the two-finger stages.

Table 2 Neonatal movement frequencies/minute to the model's gestures in Study 2

Response: Average frequency/minute (<i>SE</i>)	Model (3F – 2F)		
	BP	3F	2F
1F Incomplete	6.37 (0.70)	6.94 (0.73)	7.04 (0.78)
1F Complete	2.28 (0.39)	2.30 (0.32)	2.53 (0.37)
2F	0.83 (0.24)	0.72 (0.16)	1.42 (0.31)**
3F	0.04 (0.04)	0.42 (0.18)*	0.05 (0.02)

* $p < .05$; + $p < .10$, where first symbol is comparison to the BP, second symbol is comparison to the other condition.

Other movements

There was no significant effect of stage on the frequencies (newborn movement/minute) of the arm movements, incomplete and complete finger movements across the three stages, $F(2, 42) = 2.81$, *ns*, $F(2, 42) = 0.33$, *ns*, $F(2, 42) = 0.20$, *ns*, respectively. See Table 1 for an overview.

Duration data

See Supplementary Information 3.

Study 3: Imitation of one, two and three movements: a systematic, controlled replication

In order to further ensure that babies indeed respond selectively to all three gestures and the results were not due to an unknown order-effect, 56 further newborns were tested with all three movements, randomized in five orders (1-3-2, 2-3-1, 2-1-3, 3-1-2, 3-2-1). Six newborns were excluded due to incomplete datasets.

A sixth group received the order 1-2-3. This group of newborns was extracted from participants in Experiments 1 and 2 who all received order 1-2-3. In Experiments 1–2, the experimenter presented the model with both hands to a subset of 16 participants. These 16 newborns constituted the sixth group for testing order 1-2-3. Altogether, 66 newborns (the five new groups and the group of 16 newborns from Experiments 1–2) were included in the fourth study, and were presented the one-finger, two-finger, three-finger gestures in the six possible orders, one order per group.

Method

Participants

Sixty-six babies (39 boys, 27 girls, 30 born with vaginal delivery, 36 with caesarean section) were included in the fourth study. Their average weight was 3370 g (range: 2720–4510, $SD = 384.48$), the average gestational age was 38.84 weeks (range: 37–41, $SD = .96$), and the mean age of the babies was 1.25 days ($SD = 1.28$, 0–6 days) at the time of the examination.

Procedures

The experimental setting, equipment, coding, statistical analysis were identical to those in Study 1. All babies were presented the gestures with ‘Both’ hands, the experimenter modelled the finger movements randomly with her left and right hands throughout the experiment.

The average duration of the baseline, that preceded the demonstration of the gestures, was 104.09 seconds ($SD = 36.38$), the one-finger imitation period was 317.10 seconds ($SD = 188.07$), the two-finger imitation period was 217.43 seconds ($SD = 70.89$) and the three-finger imitation period was 224.17 seconds ($SD = 71.50$). The baseline period for the sixth group was longer than for the other groups (Means 135.95 sec ($SD = 44.36$), and 96.08 sec ($SD = 29.03$) respectively, $t = -4.02$, $p < .01$). Two independent coders coded the data and 10% of the data were reliability coded between the coders. The coders were blind to the conditions they were coding. Reliabilities were averaged and the first coder’s coding was included in the dataset. Cohen’s kappas for the frequencies in the baseline period ranged from .68 to .75, with an average of .72, while for duration data were all .92. Cohen’s kappas for frequencies in the one-finger imitation stage ranged from .75 to .83, with an average of .78, while for duration data ranged from .87 to .94, with an average of .91. Cohen’s kappas for frequencies in the two-finger imitation stage ranged from .82 to .78, with an average of .82, while for duration data ranged from .85 to .98, with an average of .90, and Cohen’s kappas for frequencies in the three-finger imitation stage ranged from .85 to .75, with an average of .78, while for duration data ranged from .90 to .96, with an average of .94.

Results

Frequency of the movements

One-finger movements. In a mixed design analysis, the frequencies of the index finger movements, incomplete index finger movements, two-finger and three-finger movements were compared in the four stages (baseline, one-finger, two-finger, three-finger) across the six orders.

A 4 (Stages: Baseline, One-Finger, Two-Finger, Three-Finger) * 6 (Order) mixed ANOVA revealed a significant main effect of *Stage*, $F(3, 180) = 13.83$, $p < .001$, $\eta_p^2 = .19$, and a significant *Stage*Order* interaction, $F(15, 180) = 1.95$, $p < .05$, $\eta_p^2 = .14$.

Post-hoc pair comparisons adjusted according to Fisher’s LSD method showed that babies significantly increased the frequencies of the one-finger extension movements in the one-finger stage compared to the baseline (Mean BP = 1.47, $SE = 0.22$, Mean 1F = 3.34, $SE = 0.35$, $p < .001$) and to the three-finger stage (Mean 3F = 2.63, $SE = 0.27$, $p < .01$). The frequencies of the one-finger movements were comparable in the one-finger and two-finger stages (Mean 2F = 3.05, $SE = 0.34$, *ns*) (see Figure 5 and Table 3).

Post-hoc comparison of the significant *Stage*Order* interaction using Bonferroni correction found a tendency

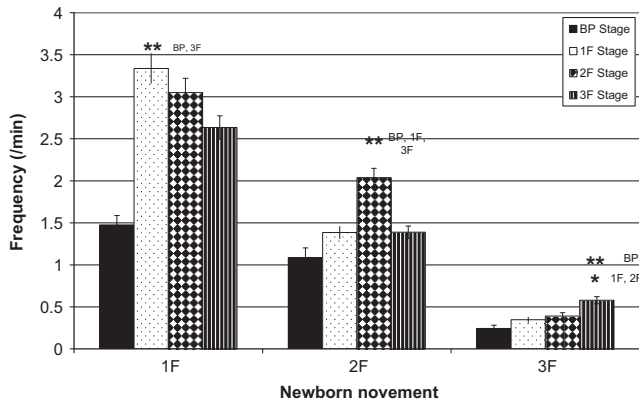


Figure 5 Study 3. Frequencies of the 1-, 2- and 3-Finger movements in the BP, and after 1-Finger, 2-Finger and 3-Finger extension models (with SE). ** $p < .01$; * $p < .05$.

Table 3 Neonatal movement frequencies/minute to the model's gestures in Study 3

Response: Average frequency/ minute (SE)	Model			
	BP	1F	2F	3F
1F	1.47 (0.22)	3.34 (0.35) a**, d**	3.05 (0.34)	2.63 (0.27)
2F	1.09 (0.23)	1.39 (0.15)	2.04 (0.22) a*, b**, d*	1.38 (0.15)
3F	0.24 (0.08)	0.34 (0.06)	0.39 (0.08)	0.58 (0.08) a**, b*, c*

* $p < .05$; ** $p < .01$, where symbols are comparison between the variable and a BP, b 1F, c 2F, d 3F conditions.

to decrease in the frequencies of the two-finger movements between the 3-1-2 and 2-1-3 orders (Mean in 3-1-2 = 5.38, $SE = 0.86$, Mean in 2-1-3 = 1.65, $SE = 0.86$, $p < .05$).

Two-finger movements. A significant main effect of *Stage*, $F(3, 180) = 6.19$, $p < .01$, $\eta_p^2 = .09$, but no significant *Stage*Order* interaction, $F(15, 180) = .92$, *ns*, was found.

Post-hoc comparisons with Bonferroni correction showed significantly higher frequencies of two-finger movements in the Two-Finger stage compared to the baseline (Mean BP = 1.09, $SE = 0.23$, Mean 2F = 2.04, $SE = 0.22$, $p < .01$) and marginally higher frequencies compared to the 1-Finger stage (Mean 1F = 1.39, $SE = 0.15$, $p = .05$), and compared to the 3-Finger stage (Mean 3F = 1.38, $SE = 0.15$, $p < .05$) (see Figure 5 and Table 3). The frequencies of the two-finger movements were comparable in the baseline, One-Finger and Three-Finger Stages.

Three-finger movements. There was a significant main effect of *Stage*, $F(3, 174) = 4.50$, $p < .01$, $\eta_p^2 = .07$, but no significant *Stage*Order* interaction, $F(15, 174) = 1.34$, *ns*. Post-hoc comparisons with Fisher's LSD adjustment showed that the frequencies of the three-finger movements were significantly higher in the three-finger compared to the baseline (Mean BP = 0.24, $SE = 0.08$, Mean 3F = 0.58, $SE = 0.09$, $p < .01$), one-finger (Mean 1F = 0.34, $SE = 0.06$, $p < .05$) and two-finger stages (Mean 2F = 0.39, $SE = 0.08$, $p < .05$) (see Figure 5 and Table 3). The frequencies of the movement were comparable across the baseline, 1-Finger and 2-Finger Stages.

See Table 4 for detailed *Stage*Order* data.

Duration data

See Supplementary Information 4.

Summary of the results

The results of Study 1a confirmed that neonates differentially imitated the raising of the index finger movement compared with the other arm and finger movement gestures when the index finger raising movement was modelled to them. The results of Studies 1b and 2 showed that babies selectively imitated the two-finger movement gestures when the two-finger movement was modelled and the three-finger movement gestures when the three-finger movement was modelled, regardless of the order of the gestures. Finally, Study 3 demonstrated that newborns selectively increased the frequencies and durations of the three modelled gestures, regardless of the order these gestures were presented. Although Table 4 shows that the dominant response across all conditions is the index finger gesture, the natural frequencies of the index finger, two-finger and three-finger conditions are not equal even at baseline periods. Even without any experimental manipulations, the index finger gesture is the most common movement, followed by the two-finger movement and then the three-finger movement. However, a comparison of the frequencies of the given movement across conditions and orders shows that the effect of selective imitation is demonstrated.

Discussion

The evidence for imitation was obtained using an objective, statistical-based analysis of the changes of the frequency and the duration of the movements, without subjective judgement on the occurrence of

Table 4 Neonatal movement frequencies/minute to the model's gestures in Study 3 according to the position of the modelled gesture

Model		Response: Average frequency/minute (SE)														
		1F condition						3F condition						BP Condition		
		1F	2F	3F	1F	2F	3F	1F	2F	3F	1F	2F	3F			
First position	1F	2.65 (0.59)	0.90 (0.21)	0.21 (0.08)	3.11 (0.60)	1.88 (0.33)	0.37 (0.13)	2.91 (0.49)	1.35 (0.22)	0.22 (0.07)	1.83 (0.37)	1.24 (0.48)	0.22 (0.09)			
	2F	2.87 (0.53)	1.36 (0.22)	0.47 (0.11)	1.79 (0.31)	1.99 (0.51)	0.31 (0.15)	2.32 (0.35)	1.31 (0.23)	0.63 (0.20)	1.02 (0.30)	1.10 (0.38)	0.21 (0.13)			
	3F	4.49 (0.70)	1.90 (0.33)	0.37 (0.13)	4.35 (0.76)	2.22 (0.31)	0.48 (0.13)	2.88 (0.29)	1.66 (0.29)	0.88 (0.19)	1.57 (0.49)	0.84 (0.28)	0.28 (0.19)			
Second position	1F	3.86 (0.76)	1.62 (0.27)	0.49 (0.14)	3.51 (0.68)	2.41 (0.48)	0.42 (0.15)	3.09 (0.56)	1.64 (0.27)	0.81 (0.20)	1.00 (0.30)	1.05 (0.39)	0.18 (0.13)			
	2F	3.03 (0.41)	1.35 (0.28)	0.24 (0.08)	3.22 (0.64)	2.05 (0.27)	0.41 (0.12)	2.76 (0.35)	1.59 (0.21)	0.52 (0.16)	1.82 (0.46)	1.08 (0.32)	0.33 (0.16)			
	3F	3.03 (0.73)	1.10 (0.23)	0.31 (0.10)	2.49 (0.53)	1.60 (0.41)	0.32 (0.14)	2.30 (0.53)	1.03 (0.25)	0.34 (0.09)	1.62 (0.36)	1.08 (0.51)	0.17 (0.10)			
Third position	1F	3.50 (0.50)	1.64 (0.30)	0.35 (0.10)	2.63 (0.59)	1.80 (0.35)	0.37 (0.13)	2.12 (0.31)	1.32 (0.25)	0.70 (0.18)	1.59 (0.48)	0.90 (0.28)	0.30 (0.18)			
	2F	4.03 (0.91)	1.36 (0.29)	0.33 (0.13)	4.21 (0.72)	2.02 (0.39)	0.43 (0.15)	3.07 (0.69)	1.36 (0.31)	0.52 (0.13)	1.59 (0.37)	1.02 (0.51)	0.139 (0.09)			
	3F	2.51 (0.41)	1.12 (0.21)	0.34 (0.09)	2.52 (0.52)	2.21 (0.41)	0.37 (0.13)	2.93 (0.36)	1.58 (0.19)	0.46 (0.17)	1.34 (0.35)	1.25 (0.39)	0.25 (0.11)			

imitation. The ethological-based coding used in these studies did not presume that babies 'respond' to the model, did not define arbitrary response times, and did not categorize the movements according to the intention of the baby. All movements the baby made were coded and analysed. The functional description of 'imitation' was used only to describe the results at the level of interpretation of the results. Therefore, the outcome measures are not absolute quantitative indicators of neonatal imitation but instead reflect the changing patterns in the distribution of the different movements of the babies according to the gesture shown to them.

Even with this approach, newborns found to be differentially increasing both the frequency and the duration of the target movements after the experimenter started modelling them, in all experiments.

The accuracy of the imitations improved over time as newborns produced increasingly accurate matches over the subsequent imitations. They displayed the first inaccurate index finger-raising movement after the experimenter's third demonstration, and it was about two demonstration periods later when they showed an accurate index finger-raising movement. They reproduced the main features of the model and they responded with matching fingers, (one, two, or three).

Given the nature of the stimuli the question can be raised whether the data support the assumption that newborns are sensitive to and respond to the numeric aspects of the stimuli. Antell and Keating (1983) reported earlier that newborns were able to keep track of the numerosity of stimuli – dishabituated looking at a picture depicting three dots after having looked at a picture with two dots. Subsequent experiments provided further evidence that infants as young as 5 month olds are sensitive to number (Feigenson, Carey & Spelke, 2002; Brannon, Abbott & Lutz, 2004, Feigenson, 2005; Wynn, 1992, 1995), and that processing small numbers is most likely based on object-based attention rather than enumeration (Feigenson & Carey, 2003). Izard, Sann, Spelke and Streri (2009) showed that newborns perceive abstract numbers. The results of the current study might provide additional evidence that neonatal infants can discriminate between small numbers of items and may possess numerical concepts as early as the first days of life.

A growing body of research supports a model in which common coding mediates the perceived action of the other and the performed action of the self. For instance, Perrett, Harries, Bevan, Thomas, Benson, Mistlin, Chitty, Hietanen and Ortega (1989) described a group of neurons in the anterior part of the superior temporal sulcus (aSTS) which has no motor properties but responds to different types of body movements and

codes goal-related behaviour (Perrett, Mistlin, Harries & Chitty, 1990). Neurons with mirror properties were described in the ventral premotor and parietal cortices of rhesus monkeys both when observing and when executing a movement (Rizzolatti, Fadiga, Gallese & Fogassi, 1996; Rizzolatti & Craighero, 2004) and goal-directed common coding takes place in the inferior frontal gyrus (IFG). According to Goldenberg and Karnath (2006), however, the common code between perception and action is based not on goals but on body parts, as they found that hand and finger movement imitations can dissociate. Patients with brain damage involving the intraparietal lobule (IPL) and middle temporal and occipital gyri show impaired hand movement imitations, whereas damage involving the IFG, insular cortex, putamen, and caudate nucleus results in impairment in finger movement imitations. These findings are incompatible with the mirror neuron system model which predicts impaired imitation following the damage of either the IPL or IFG because the integrity of both areas is necessary for intact imitative responses (Iacoboni, Woods, Brass, Bekkering, Mazziotta & Rizzolatti, 1999). The extrastriate body area (EBA) outside the mirror neuron system also contains multimodal neurons similar to those in the STS and IFG. These neurons respond when watching a body part in action, as well as to movements of the own body, when the movement is performed with the same body part even without visual input (Astafiev, Stanley, Shulman & Corbetta, 2004). Jeannerod (2004) suggested that the EBA plays a role in differentiating between the self- and other-generated movements, and using a computational model, Hafner and Kaplan (2005) proposed that the representation of one's body includes the representation of the other's body. These models of imitation, although they are diverse and represent our understanding of imitation in human adults and not newborns, might suggest the involvement of brain areas that are involved in processing the self and the other.

The results on the advantage of the left hand during imitation might suggest the involvement of a lateralized neural system. Elements of the mirror neuron system comprising the posterior inferior frontal gyrus and the posterior parietal cortex were found to be active when human adults imitated simple finger movements (Iacoboni *et al.*, 1999), mouth, hand, foot (Buccino, Binkofski, Fink, Fadiga, Fogassi, Gallese, Seitz, Zilles, Rizzolatti & Freund, 2001), or facial movements (Leslie, Johnson-Frey & Grafton, 2004), but the majority of the studies found no evidence for lateralization (Aziz-Zadeh, Koski, Zaidel, Mazziotta & Iacoboni, 2006). Study 1 and our earlier report (Nagy *et al.*, 2005) involve similar index finger movements to those employed in neuroi-

maging studies and reported a left-sided behavioural pattern that may overlap with the right-hemisphere model suggested by Goldenberg and Strauss (2002), and with models that consider imitation beyond the mirror neuron system. The infero-parietal lobule (IPL) showed a lateralized, right activation pattern when a task involved taking the perspective of the other into account (Ruby & Decety, 2001), the left IPL is activated during imitation, but the right IPL is activated when someone is imitated (Decety, Chaminade, Grezes & Meltzoff, 2002). Reciprocal imitation of finger movements activates the right IFG and left IPL (Nagy, Liotti, Brown, Waiter, Bromiley, Trevarthen & Bardos, 2010), a network that overlaps with neural structures for understanding others' intentions in relation to the self, and also may support the view that the network for imitation evolved to support interpersonal communication.

The common coding between perception and action that most of the above theories propose has been assumed as innate (Lepage & Theoret, 2007; Nagy *et al.*, 2005; Nagy, 2006), although there is no evidence for innate coding (Meltzoff & Decety, 2003). The activity of the mirror neuron system has been confirmed earliest at 6 months of age (Nyström, 2008).

Discriminative, conditioned learning (Miller & Dollard, 1941), and social learning (Bandura, 1974) models have long been proposed to explain imitative responses (see Kugiumutzakis, 1985, for review). Heyes and Ray (2000) proposed an associate sequence, a Hebbian learning model, through co-activation between sensory and motor representations, the seen movement of the other, and the executed own movements. A learning element indicated by increased accuracy of the imitations has been reported in three experiments (Field, Woodson, Cohen, Greenberg, Garcia & Collins, 1983; Nagy *et al.*, 2005; Soussignan, Courtial, Canet, Danon-Apter & Nadel, 2011), and the current data further support such claim.

The neural representations of certain motor schemas, however, might be innate. The frequent hand-mouth coordination in foetuses from 12 to 15 weeks of gestational age (deVries, Visser & Prechtl, 1984) suggests an innate neural network for oro-facial movements that are involved in feeding. The emergence of phantom limbs with congenital absence of the limbs suggests that the neural representation of some of the motor schemas involving the limbs might be innate (Gallagher, Butterworth, Lew & Cole, 1998), possibly in an experience expectant 'neural matrix' (Melzack, 1990).

In the case of a neonatal infant, sub-cortical areas are also likely to be involved in imitative actions, such as the basal ganglia that mediates early perceptual processes (Dubowitz, De Vries, Mushin & Arden, 1986; Mercuri,

Haataja, Guzzetta, Anker, Cowan, Rutherford, Andrew, Braddick, Cioni, Dubowitz & Atkinson, 1999). Reciprocity that is already present at the first imitations (Nagy & Molnar, 2004) involves additional reinforcement learning-based processes also mediated by the basal ganglia (Doya, 2000). By about 8 weeks of gestational age, the first thalamocortical, corticothalamic, and neopallium pathways, connections between the cortex, basal ganglia, and thalamus, as well as the cerebellum and brainstem, start to develop and continue developing during gestation (O’Rahilly & Müller, 1999), and although synaptic pathways will develop later, these subcortical neural structures are already in place at birth to potentially support the first imitative exchanges.

It is worth noting that all the newborns in the study were in the perinatal or early neonatal period. Neonatal refers to the period from birth to the completed 28th day of life, and the World Health Organization has further demarcated the perinatal stage within the neonatal period as a stage that lasts until the end of the seventh day after birth (WHO Geneva, WHA20.19, WHA43.27, Article 23). Developmental scientists’ debate on early imitation has rarely considered the potential importance of the exact age of the infant, and studies from the first weeks of life were frequently referred to as ‘neonatal’ imitation studies. Although no comparative data on the socio-emotional, cognitive differences in between the perinatal (0–7 days of life) and late neonatal periods (8–28 days) are available, studies on perinatal, late neonatal, and infant imitations (from 1 month on) seem to result in marked differences in their success rates. With the current study, 11 out of the 13 studies reported positive

results from the perinatal period (Field *et al.*, 1982; Kugiumutzakis, 1985; Reissland, 1998; Heimann *et al.*, 1989; Meltzoff & Moore, 1983; Nagy & Molnar, 2004; Nagy *et al.*, 2005; Field *et al.*, 1983; Meltzoff & Moore, 1989; Heimann & Schaller, 1985), while a large number of studies failed to confirm (Hayes & Watson, 1981; McKenzie & Over, 1983; Koepke, Hamm, Legerstee & Russell, 1983; Fontaine, 1984) imitation in the late neonatal period. This sharp divide raises the possibility that the early neonatal period might have some specificity regarding neonatal imitation.

Study 1 and, cumulatively, the four studies together, employed the largest sample size to date to study imitation in neonates. It is likely, although no statistical meta-analysis has confirmed it as yet, that the relatively small or small to moderate sample sizes that most studies employed, with the natural variation and rapid changes in newborns’ states and responses could have been partially responsible for prior controversial findings in the literature.

The emerging characteristics of neonatal imitation from the current study, its specificity to the features of the movement, its rapid learning component, and the possible presence of a specific period when imitation is the most likely to be reported, should be further investigated. If the perinatal, the first week of life, is indeed a specific period, and if it proves to be a sensitive period, the phenomenon might parallel the features of filial imprinting as described by Bolhuis and Honey in avian species (Bolhuis & Honey, 1998). A similar phenomenon has also been sporadically observed in the young of several mammalian species (Sluckin, 1964). Analogues between attachment and

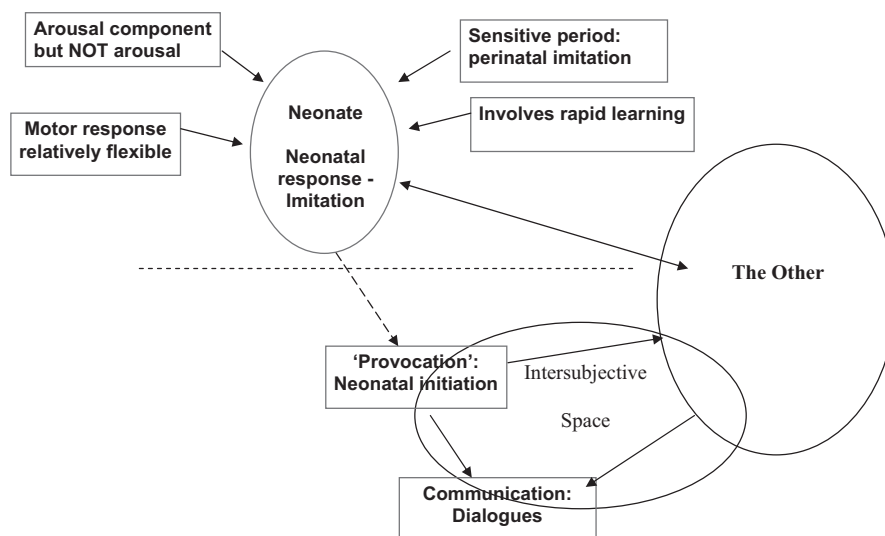


Figure 6 A contextual model of neonatal imitation.

imprinting have also been considered (Sluckin, 1964). As for imitation, ethologically based models such as releasing mechanisms (Jacobson, 1979) or biologically based universal behavioural patterns (Eibl-Eibesfeldt, 1970) and, speculatively, human imprinting (Nagy & Molnar, 1994, 2004) have been considered.

The results might allow us to speculate on a mechanism (see Figure 6) for the earliest communicative exchanges with the newborn infant. The mechanism described in this study (i) involves rapid learning, shown by the increasingly accurate one-finger imitative responses in Study 1, (ii) involves, but is not equal to, arousal, (iii) is likely to be specific to the perinatal period and (iv) the motor response follows the model's movements as indicated by the babies' ability to switch to two-finger and three-finger movements.

Neural systems subserving imitation also differentiate self- and other-generated movements (Jeannerod, 2004), and such a model might overlap with the model of a shared intersubjective space for early communication (Trevorthen, 2001). The initial imitative responses may trigger a motivational process that opens the interactional space with the other at the emergence of the intersubjectivity. This invites and keeps the caretaker within this intersubjective space that emerged through the first imitative responses. Such a mechanism in humans not only fills in the ontogenetic and phylogenetic gap for the existence of filial imprinting but also calls for a revision of our models of the emergence of the attachment systems in humans.

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References

- Abranavel, E., & Sigafos, A.D. (1984). Exploring the presence of imitation during early infancy. *Child Development*, **55**, 381–392.
- Anisfeld, M., Turkewitz, G., Rose, S.A., Rosenberg, F.R., Sheiber, F.J., Couturier-Fagan, D.A., Ger, J.S., & Sommer, I. (2001). No compelling evidence that newborns imitate oral gestures. *Infancy*, **2**, 111–122.
- Antell, S.E., & Keating, L.E. (1983). Perception of numerical invariance by neonates. *Child Development*, **54**, 695–701.
- Astafiev, S.V., Stanley, C.M., Shulman, G.L., & Corbetta, M. (2004). Extrastriate body area in human occipital cortex responds to the performance of motor actions. *Nature Neuroscience*, **7**, 542–548.
- Aziz-Zadeh, L., Koski, L., Zaidel, E., Mazziotta, J., & Iacoboni, M. (2006). Lateralization of the human mirror neuron system. *Journal of Neurosciences*, **26**, 2964–2970.
- Bandura, A. (1974). Behaviour theory and the models of man. *American Psychologist*, **19**, 859–869.
- Bard, K. (2007). Neonatal imitation in chimpanzees (Pan troglodytes) tested with two paradigms. *Animal Cognition*, **10**, 233–242.
- Bolhuis, J.J., & Honey, R.C. (1998). Imprinting, learning and development: from behaviour to brain and back. *Trends in Neurosciences*, **21**, 306–311.
- Brannon, E.M., Abbott, S., & Lutz, D.J. (2004). Number bias for the discrimination of large visual sets in infancy. *Cognition*, **93**, B59–B68.
- Buccino, G., Binkofski, F., Fink, G.R., Fadiga, L., Fogassi, L., Gallese, V., Seitz, R.J., Zilles, K., Rizzolatti, G., & Freund, H.J. (2001). Action observation activates premotor and parietal areas in a somatotopic manner: an fMRI study. *European Journal of Neuroscience*, **13** (2), 400–404.
- Decety, J., Chaminade, T., Grezes, J., & Meltzoff, A.N. (2002). A PET exploration of the neural mechanisms involved in reciprocal imitation. *NeuroImage*, **15**, 265–272.
- De Vries, J.I.P., Visser, G.H.A., & Prechtl, H.F.R. (1984). Fetal motility in the first half of pregnancy. In H.F.R. Prechtl (Ed.), *Continuity of neural functions from prenatal to postnatal life* (pp. 46–64). London: Spastics International Medical Publications.
- Doya, K. (2000). Complementary roles of basal ganglia and cerebellum in learning and motor control. *Current Opinion in Neurobiology*, **10**, 732–739.
- Dubowitz, L.M.S., De Vries, L., Mushin, J., & Arden, G.B. (1986). Visual function in the newborn infant: is it cortically mediated? *The Lancet*, **327** (8490), 1139–1141.
- Eibl-Eibesfeldt, I. (1970). *Ethology: The biology of behavior*. New York: Holt, Rinehart, Winston.
- Eyre, J.A., Miller, S., Clowry, G.J., Conway, E.A., & Watts, C. (2000). Functional corticospinal projections are established prenatally in the human foetus permitting involvement in the development of spinal motor centres. *Brain*, **123**, 51–64.
- Feigenson, L. (2005). A double dissociation in infants' representations of object arrays. *Cognition*, **95**, B37–B48.
- Feigenson, L., & Carey, S. (2003). Tracking individuals via object-files: evidence from infants' manual search. *Developmental Science*, **6** (5), 568–584.
- Feigenson, L., Carey, S., & Spelke, E. (2002). Infants' discrimination of number vs. continuous extent. *Cognitive Psychology*, **44**, 33–66.
- Field, T.M., Woodson, R., Cohen, D., Greenberg, R., Garcia, R., & Collins, K. (1983). Discrimination and imitation of facial expressions by term and preterm neonates. *Infant Behavior and Development*, **6**, 485–489.

- Field, T.M., Woodson, R., Greenberg, R., & Cohen, D. (1982). Discrimination and imitation of facial expressions by neonates. *Science*, **218**, 179–181.
- Fontaine, R. (1984). Imitative skills between birth and six months. *Infant Behavior and Development*, **7**, 323–333.
- Gallagher, S., Butterworth, G.E., Lew, A., & Cole, J. (1998). Hand–mouth coordination, congenital absence of limb, and evidence for innate body schemas. *Brain and Cognition*, **38**, 53–65.
- Goldenberg, G., & Karnath, H.O. (2006). The neural basis of imitation is body specific. *Journal of Neuroscience*, **26** (23), 6282–6287.
- Goldenberg, G., & Strauss, S. (2002). Hemisphere asymmetries for imitation of novel gestures. *Neurology*, **59** (6), 893–897.
- Hafner, V.V., & Kaplan, F. (2005). Interpersonal maps and the body correspondence problem. In Y. Demiris, K. Dautenhahn & C. Nehaniv (Eds.), *Proceedings of the third international symposium on imitation in animals and artifacts* (pp. 48–53). UK: University of Hertfordshire.
- Hayes, L.A., & Watson, J.S. (1981). Neonatal imitation: fact or artifact? *Developmental Psychology*, **17** (5), 655–660.
- Heimann, M. (2001). Neonatal imitation – a fuzzy phenomenon? In F. Lacerda, C. von Hofsten & M. Heimann (Eds.), *Emerging cognitive abilities in early infancy* (pp. 231–246). London: Erlbaum.
- Heimann, M., Nelson, K.E., & Schaller, J. (1989). Neonatal imitation of tongue protrusion and mouth opening: methodological aspects and evidence of early individual differences. *Scandinavian Journal of Psychology*, **30**, 90–101.
- Heimann, M., & Schaller, J. (1985). Imitative reactions among 14–21 day old infants. *Infant Mental Health Journal*, **6** (1), 31–39.
- Heyes, C.M., & Ray, E.D. (2000). What is the significance of imitation in animals? *Advances in the Study of Behavior*, **29**, 215–245.
- Iacoboni, M., Woods, R.P., Brass, M., Bekkering, H., Mazziotta, J.C., & Rizzolatti, G. (1999). Cortical mechanisms of human imitation. *Science*, **286** (5449), 2526–2530.
- Izard, V., Sann, C., Spelke, E.S., & Streri, A. (2009). Newborn infants perceive abstract numbers. *Proceedings of the National Academy of Sciences of the USA*, **106** (25), 10382–10385.
- Jacobson, S.W. (1979). Matching behavior in the young infant. *Child Development*, **50** (2), 425–430.
- Jeannerod, M. (2004). Visual and action cues contribute to the self–other distinction. *Nature Neuroscience*, **7**, 422–423.
- Jones, S.S. (2006). Exploration of imitation? The effect of music on 4-week-old infants' tongue protrusions. *Infant Behavior and Development*, **29**, 126–130.
- Jones, S.S. (2009). The development of imitation in infancy. *Philosophical Transactions of the Royal Society London, Series B Biological Sciences*, **364** (1258), 2325–2335.
- Kaye, K., & Marcus, J. (1978). Imitation over a series of trials without feedback: age six months. *Infant Behavior and Development*, **1**, 141–155.
- Koepke, J.E., Hamm, M., Legerstee, M., & Russell, M. (1983). Neonatal imitation: two failures to replicate. *Infant Behavior and Development*, **6**, 97–102.
- Kugiomutzakis, J. (1980). *Imitation phenomena: A new challenge*. MA thesis, Uppsala University.
- Kugiomutzakis, G. (1985). *Development of imitation during the first six months of life*. Uppsala Psychological Reports 377. Uppsala: Uppsala University.
- Kugiomutzakis, G. (1999). Genesis and development of early infant mimesis to facial and vocal models. In J. Nadel & G. Butterworth (Eds.), *Imitation in infancy* (pp. 36–59). Cambridge: Cambridge University Press.
- Lepage, J.F., & Theoret, H. (2007). The mirror neuron system: grasping others' actions from birth? *Developmental Science*, **10** (5), 513–523.
- Leslie, K.R., Johnson-Frey, S.H., & Grafton, S.T. (2004). Functional imaging of face and hand imitation: towards a motor theory of empathy. *NeuroImage*, **21**, 601–607.
- McKenzie, B.E., & Over, R. (1983). Young infants fail to imitate facial and manual gestures. *Infant Behavior and Development*, **6**, 85–95.
- Meltzoff, A.N., & Decety, J. (2003). What imitation tells us about social cognition: a rapprochement between developmental psychology and cognitive neuroscience. *Philosophical Transactions of the Royal Society, London*, **358**, 491–500.
- Meltzoff, A.N., & Moore, M.K. (1977). Imitation of facial and manual gestures by human neonates. *Science*, **198**, 75–78.
- Meltzoff, A.N., & Moore, M.K. (1983). Newborn infants imitate adult facial gestures. *Child Development*, **54**, 702–709.
- Meltzoff, A.N., & Moore, M.K. (1989). Imitation in newborn infants: exploring the range of gestures imitated and the underlying mechanisms. *Developmental Psychology*, **25**, 954–962.
- Melzack, R. (1990). Phantom limbs and the concept of a neuromatrix. *Trends in Neurosciences*, **13**, 88–92.
- Mercuri, E., Haataja, L., Guzzetta, A., Anker, S., Cowan, F., Rutherford, M., Andrew, R., Braddick, O., Cioni, G., Dubowitz, L., & Atkinson, J. (1999). Visual function in term infants with hypoxic-ischaemic insults: correlation with neurodevelopment at 2 years of age. *Archives of Diseases in Childhood*, **80** (2), F99–F104.
- Miller, N.E., & Dollard, J. (1941). *Social learning and imitation*. New Haven, CT: Yale University Press.
- Nagy, E. (2006). From imitation to conversation: the first dialogues with human neonates. *Infant and Child Development*, **15**, 223–232.
- Nagy, E., Compagne, H., Orvos, H., Pal, A.P., Molnar, P., Janszky, I., Loveland, K., & Bardos, G. (2005). Index finger movement imitation by human neonates: motivation, learning and left-hand preference. *Pediatric Research*, **58**, 749–753.
- Nagy, E., Liotti, M., Brown, S., Waiter, G., Bromiley, A., Trevarthen, C., & Bardos, G. (2010). The neural mechanisms of reciprocal communication. *Brain Research*, **1353**, 159–167.
- Nagy, E., & Molnar, P. (1994). Homo imitans or homo provocans? *International Journal of Psychophysiology*, **18** (2), 128.
- Nagy, E., & Molnar, P. (2004). Homo imitans or homo provocans? *Human imprinting model of neonatal imitation*. *Infant Behavior and Development*, **27**, 57–63.
- Nyström, P. (2008). The infant mirror neuron system studied with high density EEG. *Social Neuroscience*, **3** (3–4), 334–347.

- O'Rahilly, R., & Müller, F. (1999). *The embryonic human brain: An atlas of developmental stages* (2nd edn.). New York: Wiley-Liss.
- Perrett, D., Harries, M., Bevan, R., Thomas, S., Benson, P., Mistlin, A., Chitty, A., Hietanen, J., & Ortega, J. (1989). Frameworks of analysis for the neural representation of animate objects and actions. *Journal of Experimental Biology*, **146**, 87–113.
- Perrett, D., Mistlin, A., Harries, M., & Chitty, A. (1990). Understanding the visual appearance and consequence of hand actions. In M. Goodale (Ed.), *Vision and action: The control of grasping* (pp. 163–180). Norwood, NJ: Ablex.
- Piaget, J. (1962). *Play, dreams and imitation in childhood*. New York: Norton.
- Prechtl, H.F.R. (1974). The behavioural states of the newborn infant. *Brain Research*, **76**, 185–212.
- Reissland, N. (1988). Neonatal imitation in the first hour of life: observation in rural Nepal. *Developmental Psychology*, **24**, 464–469.
- Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annual Review of Neurosciences*, **27**, 169–192.
- Rizzolatti, G., Fadiga, L., Gallese, V., & Fogassi, L. (1996). Premotor cortex and the recognition of motor actions. *Cognitive Brain Research*, **3**, 131–141.
- Ruby, P., & Decety, J. (2001). Effect of subjective perspective taking during simulation of action: a PET investigation of agency. *Nature Neuroscience*, **4** (5), 546–550.
- Sluckin, W. (1964). *Imprinting and early learning*. London: Methuen.
- Soussignan, R., Courtial, A., Canet, P., Danon-Apter, G., & Nadel, J. (2011). Human newborns match tongue protrusion of disembodied human and robotic mouths. *Developmental Science*, **14** (2), 385–394.
- Trevarthen, C. (2001). The neurobiology of early communication: intersubjective regulations in human brain development. In A.F. Kalverboer & A. Gramsbergen (Eds.), *Handbook on brain and behavior in human development* (pp. 841–882). Dordrecht, The Netherlands: Kluwer.
- WHO Geneva, WHA20.19, WHA43.27, Article 23.
- Wynn, K. (1992). Addition and subtraction by human infants. *Nature*, **358**, 749–750.
- Wynn, K. (1995). Origins of numerical knowledge. *Mathematical Cognition*, **1**, 35–60.
- Yao, D., Yamamura, K., Narita, N., Martin, R.E., Murray, G.M., & Sessle, B.J. (2002). Neuronal activity patterns in primate primary motor cortex related to trained or semiautomatic jaw and tongue movements. *Journal of Neurophysiology*, **87**, 2531–2549.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

- Supplementary Information Study Ia.
- Supplementary Information 2. Study Ib.
- Supplementary Information 3. Study II.
- Supplementary Information 4. Study III.