

**Specialization of the motor system in infancy:  
From broad tuning to selectively specialized purposeful actions**

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## RESEARCH HIGHLIGHTS

- We provide new insights into the developmental process of motor specialization, by which motor abilities, similarly to cognitive and perceptual functions, start out broadly tuned to their goal, becoming progressively more tailored to action goals over the first year.
- During purposeful action, 9-month-old infants activated multiple redundant limbs, whereas 12-month-olds were much more likely to restrict their goal-directed movements to a single arm.
- Increased specialization of limb movements was associated with greater selective attention and motor experience.
- Our findings indicate the potential of extraneous movements for providing early motor markers of later neurocognitive deficits.

## ABSTRACT

In executing purposeful actions, adults select sufficient and necessary limbs. But infants often move goal-irrelevant limbs, suggesting a developmental process of motor specialization. Two experiments with 9- and 12-month-olds revealed gradual decreases in extraneous movements in non-acting limbs during unimanual actions. In Experiment 1, 9-month-olds produced more extraneous movements in the non-acting hand/arm and feet/legs than 12-month-olds. In Experiment 2, analysis of the spatiotemporal dynamics of infants' movements revealed developmental declines in the spatiotemporal coupling of movements between acting and non-acting hands/arms. We also showed that the degree of specialization in infants' unimanual actions is associated with individual differences in motor experience and visual attention, indicating the experience-dependent and broad functional nature of these developmental changes. Our study provides important new insights into motor development: as in cognitive domains, motor behaviours are initially broadly tuned to their goal, becoming progressively specialized during the first year of life.

**Keywords:** motor development, extraneous movements, motor overflow, specialization, infancy, reaching, action

Towards the end of the first year of life there are marked improvements in the ways in which infants use their limbs to act on the world across a range of behaviours, including manual exploration, reaching, intermanual coordination, and locomotion (e.g., Adolph & Berger, 2011; Fagard, 2000; Kimmerle, Ferre, Kotwica, & Michel, 2010; von Hofsten, 2007). Although there is general agreement amongst developmental theorists that such developments involve the increasing specificity and differentiation of the motor system in infancy (e.g., Gesell, 1954; Gibson & Pick, 2000; Thelen, 1985), the transition from a less specialized state of motor selection to one in which only relevant limbs and movements are selectively activated in the service of a goal, remains poorly understood (although see, e.g., Bhat & Galloway, 2007; Konczak & Dichgans, 1997; for consideration of the development of specialization within a limb). In this report we focus on the development of limb selection during purposeful action; specifically, we examine for the first time the progressive development of an ability to select only a single hand/arm during unimanual actions.

Previous work has shown that, in infants of 4.5-7.5 months of age (with no observed developmental changes in this period), actions with one hand are often accompanied by goal-irrelevant movements in other limbs, such as clenching, splaying, or wiggling of the fingers and toes (Soska, Galeon, & Adolph, 2012). The production of these extraneous movements in the first months of life contrasts with the skilled purposeful movements of adults and even young children. Thus we began our investigation with the hypothesis that the large prevalence of extraneous movements observed in young infants (Soska et al., 2012) may reflect a lack of specificity of the motor system, and that developmental decreases in such extraneous movements will signify the increasing specialization of the infant motor system. More specifically, we hypothesised that specialization (and thus reduction of extraneous movements) would occur particularly at the end of the first year of life, as part of the major

developments in reaching, intermanual coordination, and locomotion seen at this time (e.g., Adolph & Berger, 2011; Fagard, 2000; Kimmerle et al., 2010; von Hofsten, 2007).

In Experiment 1, we began by measuring extraneous movements in non-acting limbs during unimanual reaching, predicting a developmental decrease in such movements between 9 and 12 months of age. Experiment 1 also investigated two factors which we expected to be related to the ability to select appropriate movements in infancy: individual differences in (1) motor experience, and (2) selective attention. As described above, we were expecting decreases in extraneous movements to be specifically linked to the emergence of motor skills in which the use of the limbs is differentiated, such as cruising. Therefore, we asked parents to report on their child's motor experience. We predicted that infants' motor experience would correlate negatively with extraneous movements in task irrelevant limbs.

Selective attention is known to be closely linked to motor processes in adult humans and animals, with overlapping brain areas involved in attention shifts and movement preparation (e.g., Astafiev et al., 2003; Corbetta et al., 1998; Perry & Zeki, 2000; Rizzolatti & Camarda, 1987). It is also implicated in the modulation of extraneous movements across the life-span (Baliz et al., 2005; Soska et al., 2012; for a review see Addamo, Farrow, Hoy, Bradshaw, & Georgiou-Karistianis, 2007). We administered the "gap-overlap task" to assess goal-directed selection of visual information (Hood & Atkinson, 1993; Johnson, Posner, & Rothbart, 1991), predicting that greater difficulty with visual selection in the gap-overlap task would be associated with a higher prevalence of extraneous movements.

## Experiment 1

### Methods

#### Participants

Two age groups, 9- and 12- month-olds, were tested in this experiment. The final sample size for Experiment 1 is presented in Table 1. Six additional infants were tested but

excluded from analysis due to: i) experimenter error (one 12-month-old), ii) producing fewer than four unimanual reaches (three 9-month-olds, one 12-month-old), and iii) not reaching for objects at all (one 9-month-old). The sample size in this study was consistent with sample sizes used in comparable studies (e.g., Adolph, 2000; Bhat & Galloway, 2007). The infants were recruited via a database of parents who expressed an interest in participating in developmental studies. Ethical approval was gained from the institutional research ethics committee. Prior to testing, informed consent was obtained from all parents. Testing only took place if the infant was awake and alert. The participants were given a small gift (e.g., a T-shirt) in return for their participation.

--Table 1 about here--

### Materials and procedure

*Reaching task.* The infant was placed in an infant seat (Bébépod Flex, Prince Lionheart Inc., Santa Maria, CA, U.S.), and secured into place with adjustable straps around the waist so that movement of the trunk was restricted. There were 12 reaching trials in total. On each trial, the infant was presented with a 3.5 cm-diameter ball at the body midline, and at arm's length (calibrated for each infant) so that the infant could just grasp it without leaning forwards. The above measures were taken to prevent any potential compensatory movements in non-acting limbs resulting from changes in posture. The size of the ball was selected to induce unimanual reaching (see, e.g., Fagard, 2000). The ball's colour (white, orange, blue, green) was varied in a fixed random order between trials in order to maintain the infants' interest. Two video cameras operating at 100 Hz were used to record the infants' movements, each facing the infant either side of the midline. The movements were then coded offline.

On each trial, a coder first identified whether each reach the infant made was unimanual or bimanual using the following discrimination criteria (from Corbetta & Thelen, 1996). Unimanual reaches had to comprise a unilateral extension of one arm (the acting arm) towards the target which was followed by contact with the target. To be counted as a unimanual reach, the other non-reaching arm was required to either remain still or produce non-target-oriented movements which remained at least a fist size away from the ball. A bimanual reach was identified by bilateral extensions of the arms towards the target which contacted the target with one or both hands.

For each unimanual reach, the coder identified the timings of: i) the onset of the reach (i.e., the moment when any part of the acting hand and/or arm from the fingertips to the shoulder started a continuous trajectory which ended in target contact), and ii) contact (i.e., the moment when the hand touched the target for the first time in the trial). Next, the coder identified for each unimanual reach, whether any extraneous movement occurred. For the purpose of Experiment 1, an extraneous movement in the hand/arm was any non-target oriented movement of the non-acting hand and/or arm (from the fingertips to the shoulder) which did not come within one fist size of the target ball. Most of these movements included one or more of the following: clenching, lifting, splaying, or wiggling of the fingers, twisting of the wrist, twisting or jerking of the arms. An extraneous movement in the feet/legs was any movement in a foot and/or leg (from the toes to the hips). Most of these movements included one or more of the following: clenching, lifting, splaying, or wiggling of the toes, flexion, extension, or rotation at the ankles, rotation at the knee, jerking of the leg (Soska et al., 2012). The feet/legs never touched the target or came within one fist's size of it. If there was an extraneous movement during the reach, then we coded whether it was tightly linked to the onset of movement in the acting limb (starting +/- 100 ms around the onset of the reach of the acting hand). To compute inter-rater reliability, a second coder independently scored whether

the reach was unimanual or bimanual in 20% of all the reaches. Subsequently, the second coder scored for the presence of movement in the limbs not involved in the unimanual reach and whether they were tightly linked to the onset of the reach in 20% of the data. Inter-rater reliability was over 90%.

We calculated the proportion of unimanual reaches accompanied by extraneous movement for each infant. The measure was computed separately for the non-acting hand and the legs. Furthermore, we calculated a proportion of reaches in which extraneous movement onset was tightly linked to the onset of movement in the acting limb ( $\pm 100$  ms around the onset of the reach in the acting hand). The proportion of unimanual reaches accompanied by these reach-onset-locked extraneous movements was computed separately for hand and legs. Since these data were proportional, they were arcsine transformed prior to inferential analyses. Raw data are presented in the figures.

*Gap-overlap task.* The infant was placed on his or her parent's lap approximately 65 cm from a 20" screen. The experimenter monitored and recorded the infant's looking behaviour from an adjacent room, via a video camera. The eye movements were then manually coded offline. Before each trial, an attractive centrally-located stimulus (an "attention-getter") was displayed on the screen to attract the infant's attention. This was a square of black and white geometrical shapes changing in size (zooming in and out) accompanied by an interesting sound. Once the infant was looking at the attention-getter, the experimenter manually initiated a trial. On each trial, the attention-getter first disappeared and was replaced by a central fixation stimulus. After 800 ms, a peripheral target appeared on the left or right side of the screen and remained displayed for 1200 ms. In the Gap trials, the central fixation stimulus disappeared 200 ms prior to the onset of the peripheral target, thus leaving the screen blank for 200 ms before the appearance of the target. In the Overlap trials, the peripheral target appeared while the central fixation stimulus remained onscreen, leading

to an overlap in time between these two stimuli. The central fixation and peripheral target stimuli were selected from a pool of four stimuli (pictures of balls visually matched on colour, attractiveness, and size). The pairs of pictures were presented to the infants in a pseudorandom order. Throughout the study, each stimulus was used an equal number of times as a central fixation and a peripheral target. The central fixation and the peripheral target were never the same stimuli within any given trial.

The gap-overlap task consisted of 3 blocks. In each block, 8 Gap and 8 Overlap trials were presented, thus 16 trials in each block, and 48 trials in total. The order of presentation of the Gap and Overlap trials was randomized within each block. Trials were considered invalid if: (1) the infant did not look at the central stimulus immediately before the presentation of the peripheral target; and/or (2) the infant did not look at the peripheral target within the duration of the trial. Inter-rater reliability calculated over 20% of the data was 98% for the validity of trials and 92% for saccadic reaction times. We decided *a priori* to exclude reaction times under 150 ms or over 1200 ms (e.g., see Csibra, Tucker, & Johnson, 1998; Wass, Porayska-Pomsta, & Johnson, 2011).

Nine-month-olds contributed an average of 14 valid Gap trials ( $SD = 4.68$ ) and 13 valid Overlap trials ( $SD = 4.67$ ). Twelve-month-olds contributed on average 15 valid Gap trials ( $SD = 4.90$ ) and 14 valid Overlap trials ( $SD = 4.38$ ). The “gap effect” (the difference in reaction times between Gap and Overlap trials) was computed for each infant as a measure of efficiency of disengaging from central visual stimulus to orient to a peripheral one. Outliers below and above 2 SD were excluded from the data set. The Gap effect was 86 ms ( $SD = 39$  ms) for 9-month-olds and 81 ms ( $SD = 30$  ms) for 12-month-olds. The correlation between extraneous movements and the gap effect was run for all infants together controlling for an effect of age group.

*Motor experience.* The amount of experience with motor skills was reported by parents in a custom interview (reporting on sitting without support, crawling, standing with assistance, cruising, standing alone, walking alone; Wijnhoven et al., 2004). The parents were encouraged to use baby books, calendars, pictures, and videos to facilitate their memories (Adolph, 2002). An experimenter also tested the infants on the motor abilities listed above. A motor experience score was computed based on experience with a range of skills which were present in more than half of the infants tested in each age group. The resultant skills which were included in this measure were: sitting without support, standing with assistance, crawling, walking with assistance. The number of months' experience with each of these skills was summed for each infant to yield a "motor experience score". Outliers below and above 2 standard deviations (*SD*) were excluded from the data set. A correlation between overall proportion of unimanual reaches accompanied by extraneous movements and motor experience score was run for all participants controlling for the effect of age group.

## Results

### Reaching task

Throughout the reach, we identified significantly more extraneous movements in the non-acting hand/arm during unimanual reaching in 9-month-olds compared to 12-month-olds,  $t(36) = 3.27, p = .002, d = 1.09$  (Fig. 1a). Nine-month-olds also moved their feet/legs during a greater proportion of unimanual reaches than 12-month-olds,  $t(36) = 2.78, p = .009, d = 0.93$  (Fig. 1b).

--Figure 1 about here--

Traces of motor activity in extraneous limbs which are closely linked to the onset of purposeful movement have been observed in children and adults (Koerte et al., 2010; for a

review see Addamo et al., 2007). Such movements have been characterized as reflecting a motor command which overflows from one limb to others (Addamo et al., 2007). This “motor overflow” in children and adults is typically observed during difficult motor tasks, and very much smaller in amplitude than the extraneous movements in infants documented here and elsewhere (Soska et al., 2012). In order to investigate the presence of motor overflow in infants in this study, we examined the extent to which the infants’ extraneous movements were closely linked to reach onset by reporting extraneous movements within a window of +/- 100 ms around reach onset. Within this window, 9-month-olds continued to show a higher proportion of unimanual reaches accompanied by the onset of extraneous movements in the non-acting hand/arm than 12-month-olds,  $t(36) = 5.36, p < .001, d = 1.79$  (Fig. 1a). A trend in the same direction was also observed with extraneous leg movements,  $t(36) = 1.81, p = .078, d = 0.61$  (Fig. 1b).

#### Extraneous movements and selective attention

We found that the greater the gap effect the infants showed (i.e., the more difficulty they had with visual selection), the more overall extraneous movements they produced in their non-acting hand/arm,  $r(32) = .50, p = .002$ , controlling for age group (see Fig. 2a), but not in the feet/legs,  $r(32) = .08, p > .250$ , controlling for age group. This suggests that the processes involved in selective attention overlap with those involved in selecting an appropriate limb for action.

#### Extraneous movements and motor experience

A higher motor experience score was associated with fewer overall extraneous movements in the feet/legs,  $r(33) = -.42, p = .013$ , controlling for age group (see Fig. 2b), but not in the hand/arm,  $r(33) = .24, p = .161$ , controlling for age group. Thus, the more experience infants have with motor skills, the more specialized their reaching movements are (i.e., the less they activate their lower limbs when not goal-appropriate).

--Figure 2 about here--

### Experiment 2

Experiment 1 revealed a developmental decrease in extraneous movements during reaching between 9 and 12 months of age. We also observed that a large proportion of 9-month-olds' unimanual reaches were accompanied, at their onset ( $\pm 100$  ms), by extraneous movements in the non-acting hand. These onset-locked movements are likely the developmental precursor of the motor overflow seen in older children and adults during demanding actions (Addamo et al., 2007).

In adults, it has been argued that symmetrical control of the two hands is surmounted via inhibitory processes (Dennis, 1976; Duque et al., 2007). If symmetrical activation of the hands is, as some have suggested (e.g., Fagard, 1998; Goldfield & Michel, 1986; Goldfield & Wolff, 2004), a general principle of action in early infancy, we should also see more symmetrical spatiotemporal congruency between acting and non-acting hands in young infants compared to older infants. Experiment 2 tested this hypothesis by examining the spatiotemporal congruency between the acting and non-acting hands/arms. Using motion capture, we measured in fine detail the spatiotemporal coupling between movements in acting and non-acting hands/arms during the action of shaking a rattle with a single hand in 9- and 12-month-olds. We predicted the presence of spatiotemporal coupling (symmetrical about the body midline) in 9-month-olds, which would be significantly reduced in 12-month-olds. A key advantage of the rattling action is that it allows greater confidence that any extraneous movements are an unintended outcome of the action. Many studies of reaching behaviour (Experiment 1 included) have to make assumptions about whether infants intended the reach

towards objects to be with one or two hands (see Fagard & Pez , 1997). With rattle shaking, intention to act bimanually is extremely unlikely.

In adults, the interhemispheric inhibition responsible for suppressing bilateral motor activation is down-regulated as the effort required for a motor response increases (Perez & Cohen, 2008; Tinazzi & Zanette, 1998). Thus, we also investigated in the infants the effect of effort (speed of shaking) (Bodwell, Mahurin, Waddle, Price, & Cramer, 2003; Morrison, Hong, & Newell, 2011) on spatiotemporal congruency during rattle shaking. If increased speed of shaking is related to increases in between-arm congruency in infants, this would suggest that the developmental suppression of extraneous movements in infancy is driven at least in part by inhibitory processes.

## Methods

### Participants

The 9- and 12-month-olds recruited for Experiment 1 were also asked to participate in Experiment 2. The sample size for Experiment 2 is presented in Table 1. In Experiment 2, ten infants (in addition to those reported in Table 1) were tested but excluded from analysis because: i) they produced fewer than four shaking sequences (six 9-month-olds, two 12-month-olds) and ii) due to equipment failure (one 9-month-old, one 12-month-old). The sample size in this study was consistent with sample sizes used in comparable studies (e.g., Adolph, 2000; Bhat & Galloway, 2007).

### Procedure and materials

In Experiment 2, the infant was placed in the same infant seat as used in Experiment 1, and secured with adjustable straps around the waist so that movement of the trunk was restricted. The rattle (which was 19 cm in length, and 6.7 cm in diameter at its widest point) was presented to the infant. Following extensive piloting with several types of rattle, this particular rattle was selected as being the one which produced the greatest amount of

unimanual shaking in the infants. We alternated between giving the infants each of two different versions (one was opaque, the other transparent, but they were otherwise identical) of the same rattle in order to maintain their engagement in the task. At the beginning of each trial, the experimenter demonstrated the shaking of a rattle and placed the rattle in the infant's left or right hand to facilitate unimanual shaking. The side of presentation was presented in a novel pseudorandom order for each participant (with the constraint that the rattle could not be placed in the same hand more than twice consecutively). There were 6 shaking trials in total, each lasting 30 seconds.

Movement of the arms during shaking was recorded using an eight-camera OptiTrack motion capture system operating at 100 Hz (NaturalPoint, Inc., Corvallis, OR, U.S.). Six of the cameras recorded position–time data from both arms while two cameras served as video cameras (100 Hz). This allowed us to obtain motion capture data synchronized with video footage. Cameras were placed surrounding the infant. The reference frame of the system was set relative to the infant, such that the  $x$ -axis (horizontal) corresponded to the left-right axis of the body (left shoulder to right shoulder). We observed very little trunk rotation, which might otherwise have misaligned the body left-right axis with the reference  $x$ -axis. Likewise, the  $y$ -axis (vertical) corresponded to the vertical axis of the body, and we observed very little forward trunk sway which might otherwise have misaligned the body and room vertical axes.

To capture the position of the arms, two custom-made rigid bodies were constructed. Each was made up of an array of four reflective markers (each 15.88 mm in diameter) placed in fixed positions on a small non-reflective plastic board (550 x 550 mm). The rigid bodies were each mounted on a velcro strap which was used to secure them to the infants' forearms (one on each arm).

From the video records, the coder selected unimanual shaking sequences which were at least 2 seconds long, when one hand was shaking the rattle on one side of body while the

other hand was not touching the rattle and free to move on the other side of the body. The motion capture data were analysed offline. At each frame the 3D positions of the centre of each of the rigid bodies were calculated using the system's analysis software ("Tracking Tools", NaturalPoint Inc., Corvallis, OR, U.S.). Further analyses were performed with customized Matlab routines (Mathworks Inc., Natick, MA, U.S.). For each shaking sequence, the position of the centre of the rigid body on  $x$ -,  $y$ -, and  $z$ -axis was plotted and then visually inspected to identify shaking sequences which did not contain sufficient data for further analysis (e.g., due to occlusion of motion capture markers). Segments of data with significant artefacts (e.g., spikes) were detected visually and deleted. Next, the data were interpolated using a cubic spline function and filtered using a second-order low pass Butterworth filter operating at 8 Hz.

As a measure of spatiotemporal congruency between the arms, we calculated the correlation between the positions of the acting and non-acting arms on the horizontal ( $x$ ) and vertical ( $y$ ) axes for every shaking sequence (following Fagard & Pez , 1997). We focused on the  $x$ - and  $y$ -axes, because shaking did not typically involve significant movement in depth (the  $z$ -axis). On the vertical ( $y$ ) axis, a higher positive correlation indicates greater spatiotemporal congruency (e.g., as one arm moves up, the other also moves up, see Fig. 3a). On the horizontal ( $x$ ) axis, negative correlations indicate greater spatiotemporal symmetry about the body midline (e.g., as one arm moves right, the other moves left, see Fig. 3b). Outliers above and below 2  $SD$  were excluded from the data set. Because the data were bounded between -1 and 1, they were arcsine transformed. The raw data are presented in the figures. The average speed of the shaking arm was also computed for each shaking sequence. In order to examine the role of shaking speed in spatiotemporal coupling between acting and non-acting arm movements, a median split ( $Mdn = 287$  mm/sec) was performed on speed of the shaking arm to divide shaking sequences into a slower half ( $M = 187$  mm/sec,  $SD = 64$

mm/sec; henceforth “slow”) and a faster half ( $M = 431$  mm/sec,  $SD = 120$  mm/sec; henceforth “fast”).

Correlations in the vertical and horizontal axes for every sequence were used in the statistical analyses. In total, 242 unimanual shaking sequences were used for the statistical analyses (9-month-olds: 126 shaking sequences; 12-month-olds: 116 shaking sequences). On average, each 9-month-old contributed 9 shaking sequences ( $SD = 5.88$ ). Each 12-month-old contributed on average 6 shaking sequences ( $SD = 4.86$ ).

## Results

### Vertical axis

The shaking sequences were entered into a 2 x 2 analysis of variance (ANOVA) examining the effect of Age (9- versus 12-month-olds) and Speed (of the acting arm; slow versus fast) on correlation scores in the vertical axis. The ANOVA revealed a main effect of Age, indicating more positive correlation scores in the shaking sequences of 9-month-olds than those of 12-month-olds,  $F(1, 238) = 6.90, p = .009, \eta_p^2 = .03$ . Furthermore, there was a main effect of Speed indicating that correlation scores were more positive with speed,  $F(1, 238) = 20.51, p < .001, \eta_p^2 = .08$ . There was also an interaction between Age and Speed,  $F(2, 238) = 8.07, p = .005, \eta_p^2 = .03$ . At a slow speed, 9-month-old’s shaking sequences showed more positive correlation scores than those of the 12-month-olds,  $t(119) = 3.57, p = .002, d = 0.66$  ( $p$ -value Bonferroni corrected) (see Fig. 3c). But there was no significant difference between Ages for fast speed. While 9-month-olds did not show a difference in correlation scores between slow and fast speed movements, correlation scores at 12 months were significantly more positive for fast speed compared to slow speed movements,  $t(114) = 4.56, p < .001, d = 0.87$  ( $p$ -value Bonferroni corrected) (see Fig. 3c).

One-sample  $t$ -tests of correlation scores against zero (i.e., no correlation; see Fig. 3c) revealed that correlation scores were significantly more positive than 0 for both slow and fast

speeds in 9-month-olds,  $t(51) = 3.17, p = .012, d = 0.44$ ;  $t(73) = 6.52, p < .001, d = 0.76$  ( $p$ -value Bonferroni corrected). This was also true for 12-month-olds, but only for fast speed movements,  $t(46) = 4.58, p < .001, d = 0.67$  ( $p$ -value Bonferroni corrected).

#### Horizontal axis

The shaking sequences were entered into a 2 x 2 ANOVA examining the effect of Age (9- versus 12-month-olds) and Speed (of the acting arm; slow versus fast) on correlation scores in the horizontal axis. The ANOVA revealed a main effect of Age, indicating more positive correlation scores in the shaking sequences of 9-month-olds than those of 12-month-olds,  $F(1, 238) = 9.01, p = .003, \eta_p^2 = .04$ . There was no main effect of speed or interaction between Age and Speed.

One-sample  $t$ -tests of correlation scores against zero (i.e., no correlation; see Fig. 3d) revealed that correlation scores were significantly negative with respect to zero for fast speed movements in 9-month-olds,  $t(73) = 2.72, p = .032, d = 0.32$  ( $p$ -value Bonferroni corrected). But slow movements in 9-month-olds and both slow and fast movements in 12-month-olds were not significantly different from zero.

--Figure 3 about here--

#### General discussion

We have documented for the first time a substantial decrease in extraneous movements accompanying unimanual object-directed reaching between 9- to 12-months of age (Experiment 1). This developmental trend is reflected in a simultaneous decrease in the spatiotemporal congruency of movements between the arms during unimanual shaking (Experiment 2). We argue that both findings reflect a wider developmental process of gradual motor specialization over the first year of life, in which infants' motor responses to action

goals become increasingly tailored to their purpose, resembling the developmental processes of specialization seen in other domains including language and face processing (Gervain & Mehler, 2010; Lewkowicz & Ghazanfar, 2009; Maurer & Werker, 2014; Pascalis et al., 2005; Scott & Monesson, 2010; Werker & Tees, 1984; for a review see Johnson, 2011).

What developmental processes underlie this motor specialization? As argued earlier, the increases in inter-limb congruency with speed observed in Experiment 2 point to a role for inhibition in the modulation of extraneous movements (Addamo et al., 2007; Hoy, Fitzgerald, Bradshaw, Armatas, & Georgiou-Karistianis, 2004; Perez & Cohen, 2008). It may be that brain changes underlying the development of inhibitory connections between two hemispheres can explain the decreases in extraneous movements observed in Experiments 1 and 2. The main brain structure responsible for interhemispheric inhibition is the corpus callosum, and this develops across early life reaching its adult size and myelination in later adolescence when extraneous movements typically decline to an adult level (for a review see Addamo et al., 2007; Giedd et al., 1999). It has also been implicated in the development of a range of motor behaviours including intermanual coordination and laterality (Muetzel et al., 2008; Sacco, Moutard, & Fagard, 2006). However, it is very likely that other changes in motor circuits (e.g., pruning in ipsilateral corticospinal projections; Eyre, Taylor, Villagra, Smith, & Miller, 2001; Martin, 2005) contribute to explaining the wider range of changes in motor specialization.

In adults, the brain areas involved in movement preparation overlap substantially with those implicated in selective attention (Astafiev et al., 2003; Corbetta et al., 1998; Perry, 2000; see also Allport, 1989; Rizzolatti & Camarda, 1987). Here, we found that infants with a greater ability to disengage from a familiar visual stimulus and shift attention to a new event were better able to produce movements more specifically tailored to their action goals (i.e., fewer extraneous movements), indicating an overlap in early life between processes of

selective attention and movement (e.g., Bacher & Robertson, 2001; Robertson & Johnson, 2009). The emerging ability to shift attention between sensory stimuli which occurs during the first months of life (Colombo, 2001; Richards & Casey, 1992) likely provides the crucial foundation for the selective processes required in the motor skills, which continue to be perfected well beyond infancy (Addamo et al., 2007; Koerte et al., 2010).

Finally, our finding of a link between greater motor experience and fewer extraneous foot movements suggests that motor specialization (as with specialization in other domains; Johnson, 2011) is an experience-dependent process. The particular coupling between motor skills and extraneous movements of the feet reinforces the view that motor learning is specific to the mode of action (Adolph, 2000). Further research will be needed to determine how motor experience interacts with the neural mechanisms described above and which, we suggest, underlie the development of motor specialization. A better understanding of the developmental processes underlying motor specialization has great clinical significance since aggravated extraneous movements have been described in various clinical populations including children with attention-deficit/hyperactivity disorder (e.g., D'Agati, Casarelli, Pitzianti, & Pasini, 2010; MacNeil et al., 2011) and autism (e.g., Jansiewicz et al., 2006).

Why do infants produce extraneous movements during purposeful action? In fact we consider it highly likely that, far from being extraneous, such movements serve adaptive purposes in early life. It may be that such movements are a vestige of our evolutionary past. Movements in the legs during reaching and manipulation (Soska et al., 2012) could be driven by a phylogenetically older, quadrupedal system of movement (see Dietz, 2002). The dramatic decline in such extraneous leg movements observed here may thus signify the progression to a more recently evolved mode in which the manual system operates independently of quadrupedal movement. Irrespective of this, it is likely that extraneous movements also play an adaptive role in ontogenetic development. It may be that the broad

motor tuning provided by extraneous movements facilitates specialization by enabling the selection of the most efficient movements for a given action as sensorimotor experience progresses. A further possibility is that extraneous movements provide motor activity and reafferent sensory feedback which is crucial to activity dependent processes of development in the nervous system (see Blumberg, 2015).

The current paper provides important new insights into the processes whereby infants become able to select appropriate limb movements in the service of purposeful action. In the early stages of learning to act on the world, the infant motor system appears to be “broadly tuned”, but over the first year of life, motor responses become progressively more specialized. We argue that this broad motor tuning in early infancy likely fulfils an adaptive function by providing young infants with a wide repertoire of responses to their environment from which they can select the most effective over the coming months of life. The process of motor specialization documented here has wide-reaching implications for the development of a range of motor abilities such as object exploration, locomotion, intermanual coordination, the emergence of lateralised action, and tool use.

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## LIST OF FIGURE LEGENDS

Figure 1: Experiment 1. Proportion of unimanual reaches accompanied by movements in non-reaching limbs, for 9- and 12-month-olds. (a) Overall movements observed in the non-acting hand throughout the reach, and movements in the non-acting hand/arm with an onset that is tightly linked to the onset of the reach ( $\pm 100$ ms). (b) Overall movements in the feet/legs throughout the reach, and movements in the non-acting feet/legs with an onset that is tightly linked to the onset of the reach ( $\pm 100$ ms). Error bars show  $\pm 1$  SE, \*  $p < .050$ , \*\*  $p < .010$ , \*\*\*  $p < .001$ .

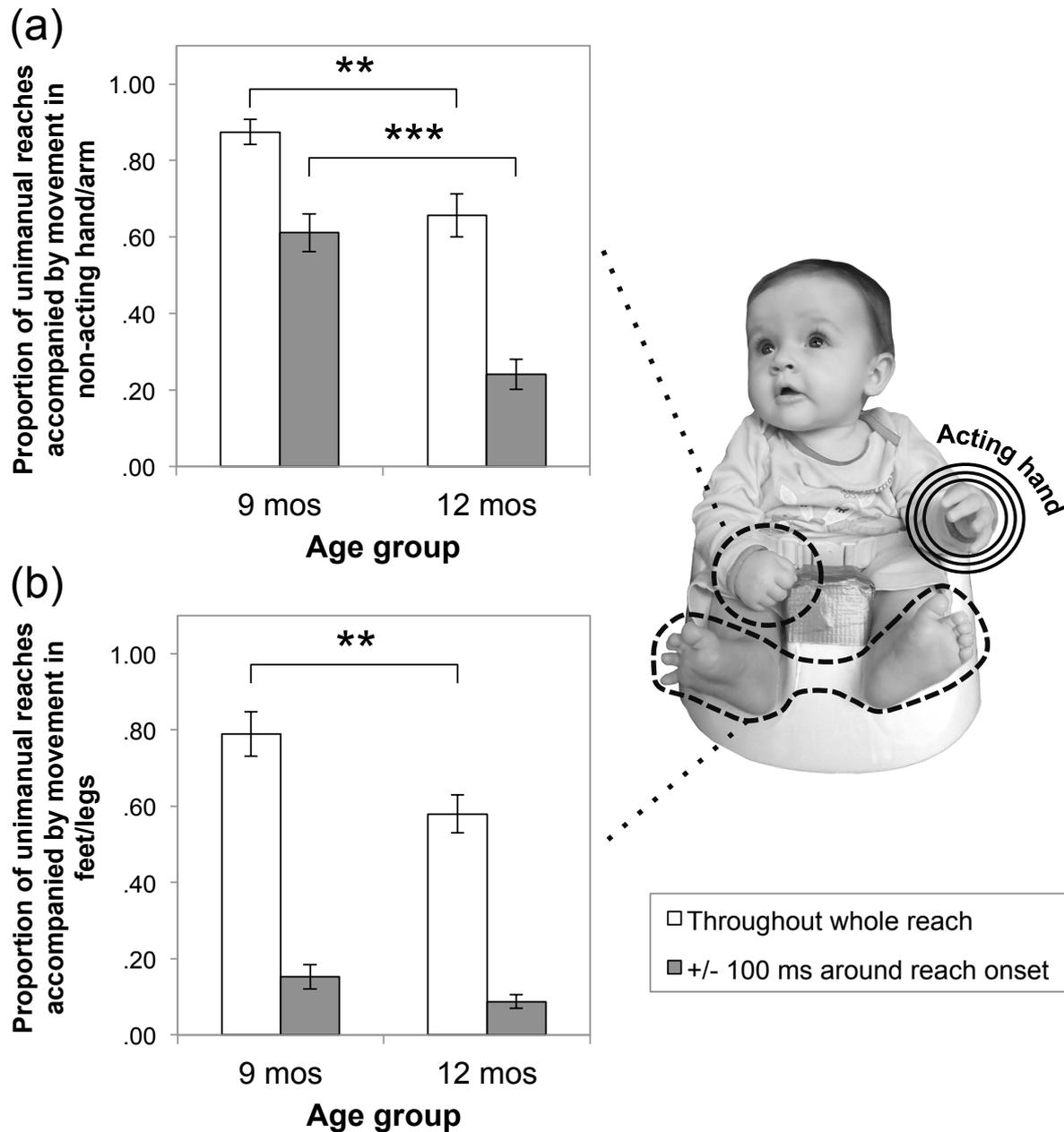
Figure 2: Experiment 1. Associations between extraneous movements and measures of selective attention and motor experience. (a) Partial correlation scatterplot showing a positive association between performance on the gap-overlap attention task and the overall proportion of reaches with movement in the non-acting hand/arm. The longer it takes infants to visually select a target, the more they produce extraneous movements in their non-acting hand/arm. (b) Partial correlation scatterplot showing a negative association between proportion of unimanual reaches with movement in feet/legs and motor experience. The more motor experience infants have, the less they produce extraneous movements in their feet/legs.

Figure 3: Experiment 2. Correlation scores for unimanual rattle-shaking movements. (a) An example of a rattle-shaking sequence where acting and non-acting arms show large positive correlation on the vertical ( $y$ ) axis indicating that they were moving up and down in synchrony (the correlation between positions of the arms is .92). (b) An example of a rattle-shaking sequence where acting and non-acting arms show moderate negative correlation on the horizontal ( $x$ ) axis indicating that they were moving in symmetry about the midline (the

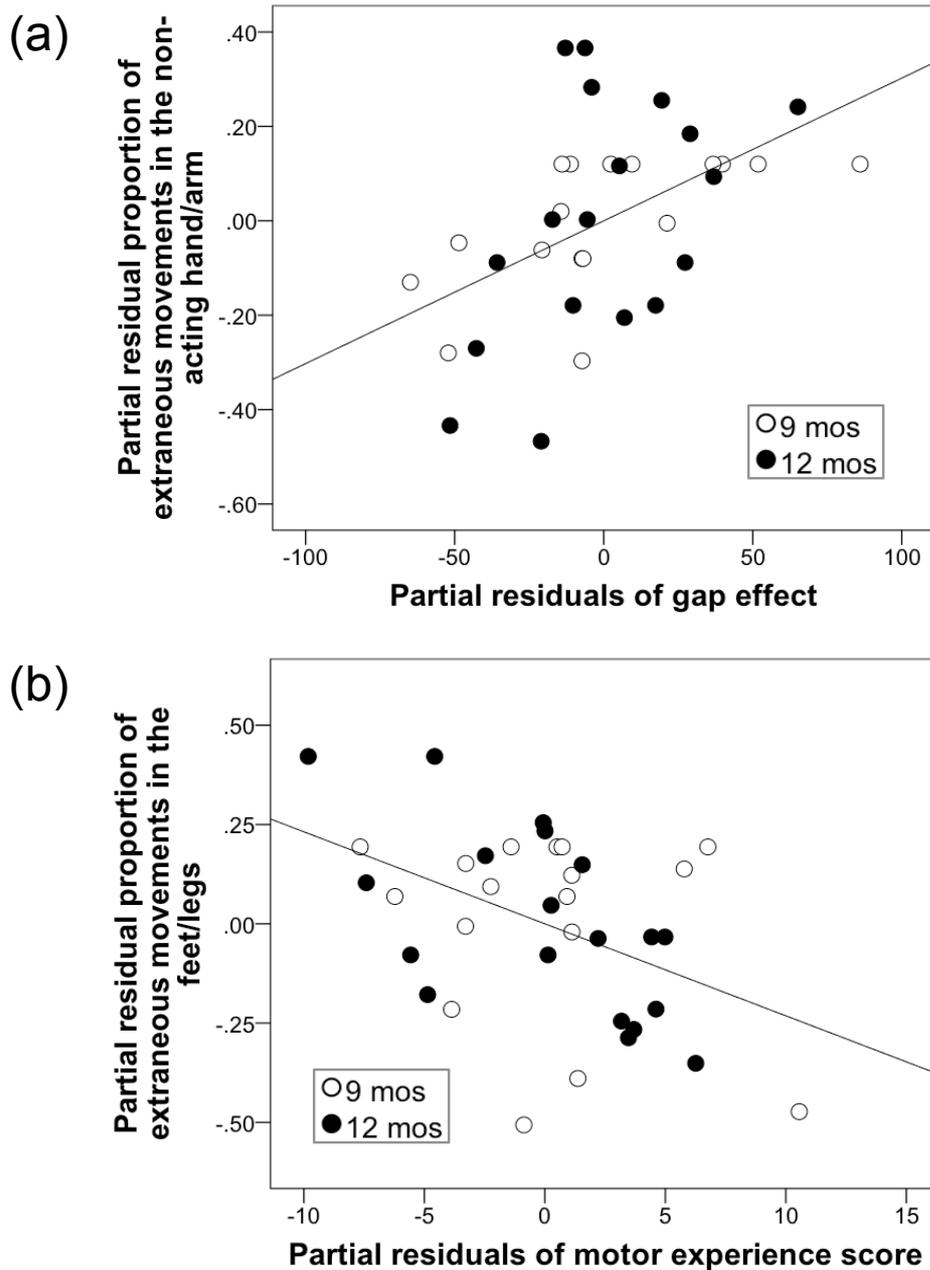
correlation between positions of the arms is  $-.39$ ). (c) Correlation scores on the vertical axis during shaking in 9- and 12-month-olds for slow speed (white bars) and fast speed (grey bars) of shaking. (d) Correlation scores on the horizontal axis during shaking in 9- and 12-month-olds for slow speed (white bars) and fast speed (grey bars) of shaking. Error bars show  $\pm 1$  SE, \*  $p < .050$ , \*\*  $p < .010$ , \*\*\*  $p < .001$ .

Table 1: Participant characteristics in Experiments 1 and 2

|                     | Age group     | n  | Sex     | Mean age (months)         |
|---------------------|---------------|----|---------|---------------------------|
| <b>Experiment 1</b> | 9-month-olds  | 18 | 9f, 9m  | 8.88 ( <i>SD</i> = 0.30)  |
|                     | 12-month-olds | 20 | 8f, 12m | 12.14 ( <i>SD</i> = 0.32) |
| <b>Experiment 2</b> | 9-month-olds  | 14 | 8f, 6m  | 8.90 ( <i>SD</i> = 0.31)  |
|                     | 12-month-olds | 19 | 7f, 12m | 12.19 ( <i>SD</i> = 0.28) |



**Figure 1:** Experiment 1. Proportion of unimanual reaches accompanied by movements in non-reaching limbs, for 9- and 12-month-olds. (a) Overall movements observed in the non-acting hand throughout the reach, and movements in the non-acting hand/arm with an onset that is tightly linked to the onset of the reach ( $\pm 100$ ms). (b) Overall movements in the feet/legs throughout the reach, and movements in the non-acting feet/legs with an onset that is tightly linked to the onset of the reach ( $\pm 100$ ms). Error bars show  $\pm 1$  SE, \*  $p < .050$ , \*\*  $p < .010$ , \*\*\*  $p < .001$ .



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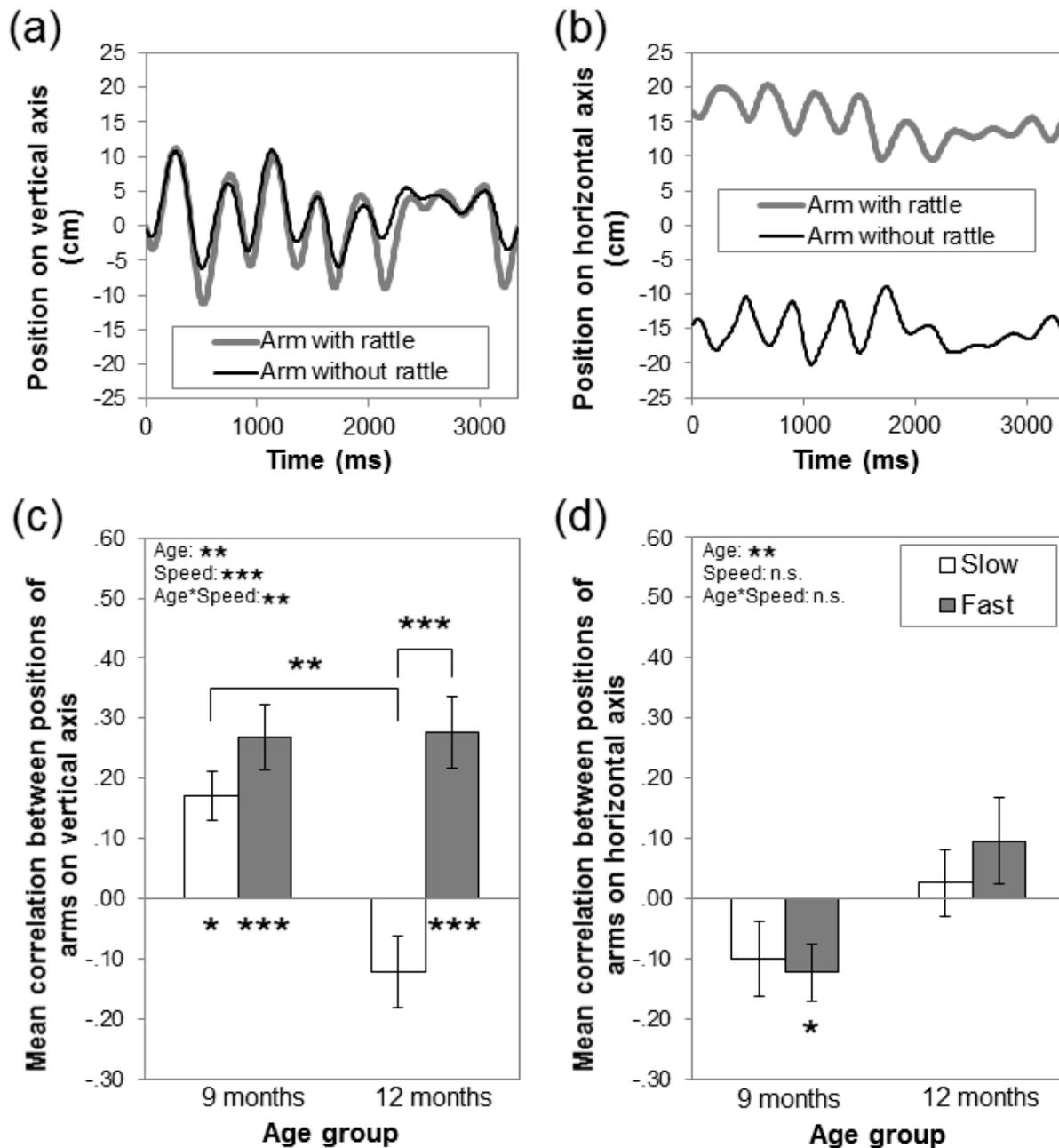


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