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Infants' observation of others' actions: Brief movement-specific visual experience primes motor representations

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Recent research suggests that infants' observation of others' reaching actions activates corresponding motor representations which develop with their motor experience. Contralateral reaching develops a few months later than ipsilateral reaching, and 9-month-old infants are less likely to map the observation of these reaches to their motor representations. The goal of the current study was to test whether a brief familiarization with contralateral reaching is sufficient to prime this less developed motor representation to increase the likelihood of its activation. In Experiment 1, infants were familiarized with contralateral reaching before they were tested in an observational version of the A-not-B paradigm. A significant number of infants searched incorrectly, suggesting that the observation of contralateral reaching primed their motor representations. In Experiment 2, infants were familiarized with ipsilateral reaching, which shared the goals but not the movements associated with the contralateral reaches observed during testing, and they did not show a search bias. Taken together, these results suggest that a brief familiarization with a movement-specific behaviour facilitates the direct matching of observed and executed actions.

The first year of life affords infants many opportunities to learn about themselves, other people, and their surroundings. Much of this learning occurs from observing the movements and effects of their own as well as others' actions. Interestingly, it is often reported that during this period of development, infants' perception and production of actions are coupled (Bertenthal & Longo, 2008; Hauf, 2007; Lepage & Théoret, 2007; Paulus, Hunnius, Vissers, & Bekkering, 2011; Rakison & Woodward, 2008; Sommerville, Woodward, & Needham, 2005; van Elk, van Schie, Hunnius, Vesper & Bekkering, 2008). For instance, infants interpret others' manual reaches as goal directed by 5–6 months of age (Király, Jovanovic, Prinz, Aschersleben, & Gergely, 2003; Woodward, 1998), which corresponds with when they begin to successfully reach for distal objects (Bertenthal & von Hofsten, 1998). Similarly, the sorts of grasps 6-month-old infants perform predict their ability to differentiate others' grasps (Daum, Prinz, & Aschersleben, 2011). At 10 months of age, infants who are capable of pulling a cloth to retrieve a toy are more likely to understand the means-end structure of someone else performing the same goal-directed

action (Sommerville & Woodward, 2005). The most parsimonious interpretation for these findings is that there is a bidirectional developmental relation between the perception and execution of actions (e.g., Daum, Prinz, & Aschersleben, 2009; Hauf, 2007).

These findings were anticipated by James's (1890) and Greenwald's (1970) ideomotor theories, and more recently Prinz's (1997) common coding theory. According to these theories, action perception and production share representational resources, and, thus, observed events facilitate or interfere with one's own coinciding actions (Hommel, Musseler, Aschersleben, & Prinz, 2001). The discovery of mirror neurons in non-human primates, and homologous findings in humans (e.g., Decety *et al.*, 1997; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996), provides further support for this theory. In essence, it is hypothesized that observed actions are mapped to corresponding motor representations in the observer's brain (see Rizzolatti & Craighero, 2004; Rizzolatti & Sinigaglia, 2010).

Considerable electrophysiological, neuroimaging, and behavioural evidence supports this direct matching hypothesis that action observation activates motor representations in adults (see Heyes, 2011 for a review). For instance, adults show similar patterns of EEG mu rhythm desynchronization when they perform or observe others perform goal-directed actions (Nishitani & Hari, 2000), which has also been found with 8- to 14-month-old infants (e.g., Marshall, Young, & Meltzoff, 2011; Nyström, Ljunghammar, Rosander, & von Hofsten, 2011; Southgate, Johnson, El Karoui, & Csibra, 2010). Additional observational and eye tracking studies suggest that infants mirror or match observed actions that they are capable of executing (e.g., Daum *et al.*, 2009, 2011; Hamlin, Hallinan, & Woodward, 2008). These shared representations enable infants to understand observed actions as well as to predict the goals or effects of these actions (Cannon, Woodward, Gredebäck, von Hofsten, & Turek, 2012; Henrichs, Elsner, Wilkinson, Elsner, & Gredebäck, 2014; see Gredebäck & Falck-Ytter, in press, for a review), and infants' motor experience is an important contributor to this developmental outcome (see Woodward & Gerson, 2014 for a review).

Longo and Bertenthal (2006) conducted a study that suggested that 9-month-old infants represent ipsilateral and contralateral reaching differently specifically because of differences in motor experience. In brief, they tested infants in Piaget's A-not-B search task: Infants observe an object hidden in one of two locations (A-location), and then search for it. After a few trials, the experimenter hides the object in the other location (B-location), and the infant searches again. Infants between 8 and 12 months of age typically err and search at the A-location rather than at the B-location, which is one of the most well studied and replicable findings in developmental psychology (e.g., Marcovitch & Zelazo, 1999; Wellman, Cross, & Bartsch, 1986). Whereas Piaget (1937/1954) suggested this is due to infants' fragile understanding of object permanence, more recent accounts suggest that repeated reaches to the A-location establish a response bias that infants are unable to inhibit (Clearfield, Dineva, Smith, Diedrich, & Thelen, 2009; Diamond, 1985, 1991; Diedrich, Thelen, Smith, & Corbetta, 2000; Smith, Thelen, Titzer, & McLin, 1999; Thelen, Schöner, Scheier, & Smith, 2001; Zelazo, Reznick, & Spinazzola, 1998).

Longo and Bertenthal (2006) replicated this finding but also tested infants in an observation version of the A-not-B task, in which infants watched the experimenter repeatedly hide and retrieve the object on the A-trials, and were only allowed to search for the object on the B-trial. If overt reaching was necessary to bias infants to search incorrectly, then infants should not commit a search error. If, however, infants mapped the observed actions to their motor representations, then infants may commit a search error. Interestingly, a search error was observed, but only if the experimenter hid and retrieved the object during the A-trials with his ipsilateral hand (i.e., same side of the body

as the object); infants searched randomly if the experimenter used his contralateral hand (i.e., opposite side of the body as the object).

This interaction with reach type was unexpected, but suggested the importance of considering both the means and the goals when evaluating infants' action understanding. Although sometimes overlooked in the infant literature, it is important to appreciate that actions are represented at multiple levels that can include their means, their goals, or both (Decety, 1996; Hommel, 1996). In the search task, the goal was always the same (i.e., retrieve the hidden object), but the means (i.e., ipsilateral or contralateral reach) differed. Critically, the development of contralateral reaching generally lags 2–4 months behind ipsilateral reaching (Bruner, 1969; Morange & Bloch, 1996; Provine & Westerman, 1979). Infants tend not to spontaneously reach contralaterally until about 26 weeks of age (van Hof, van der Kamp, & Savelsbergh, 2002), and the frequency of spontaneous contralateral reaching remains very low throughout the first year. Even when infants are tested in situations designed to constrain ipsilateral reaching, the frequency of contralateral reaching at 9 months of age is only 15–25% (Barton & Bertenthal, 2013; Gampe, Keitel, & Daum, 2015; Melzer, Prinz, & Daum, 2012). This suggests that infants have relatively limited experience performing contralateral reaches during the first year, and thus, their motor representation would be less well developed than that for ipsilateral reaching. As such, they would be less likely to map a contralateral reach to a motor representation and develop a response bias during the search task.

One critical question, which has not yet been addressed, is whether the activation of a motor representation during action observation varies exclusively as a function of long-term experience, or alternatively, could it be influenced by the infant's recent experience as well? Accordingly, in the current study, we examine whether providing infants with experience observing an experimenter repeatedly reaching during a familiarization period affects performance on a subsequent observational A-not-B search task. In Experiment 1, infants observed an experimenter reaching only contralaterally for toys during familiarization, whereas in Experiment 2, infants observed an experimenter reaching only ipsilaterally during familiarization. In both experiments, the subsequent observational A-not-B search task was conducted exclusively with contralateral reaches. Infants' familiarization with contralateral reaching in Experiment 1 could prime both the goal and the movement associated with the motor representation of the contralateral reach they subsequently observed at test. By contrast, familiarization with ipsilateral reaching in Experiment 2 could prime the goal associated with the motor representation, but not the specific movement, due to the difference between the ipsilateral and contralateral reaching movements observed during familiarization and test. By including both familiarization conditions, we were able to test whether the motor representation could be primed by infants observing the goal of the action, the movement of the action, or both.

EXPERIMENT 1

In this experiment, 9-month-old infants observed the experimenter repeatedly performing contralateral reaches for objects during a familiarization phase, followed by the observational version of the A-not-B search task. Whereas previous research suggests that infants do not show a search error at this age when the experimenter reaches contralaterally (Longo & Bertenthal, 2006), we hypothesized that the familiarization experience would prime motor activation during the search task, and thus result in a search error on the B-trial of the task.

Method

Participants

Thirty 9-month-old infants participated (M = 275.8-days, SD = 8.7-days; 17 females, 13 males).[1] An additional three infants were tested, but were excluded due to fussiness (1), ambiguous search behaviour (1), or parental interference (1). Participants were primarily from middle-class families and were predominantly Caucasian. We obtained contact information through birth records and community outreach and contacted parents by mail, phone, or e-mail. We gave parents an overview of the procedure, and they signed a consent form before the study began. All infants were given a gift of appreciation after participating.

Materials

Six plastic toys were used during the familiarization phase, another toy was used during the training trials, and an additional toy that rattled when shaken was used during the A and B test trials, which is consistent with a previous study that adopted a similar experimental sequence (Boyer, Pan, & Bertenthal, 2011). The training apparatus consisted of a box (41 × 32 × 4.3 cm) with a single cylindrical well set in its centre (12 cm diameter). A similar apparatus, with two cylindrical wells, 12.7 cm apart, was used for the test trials. Cylindrical lids with spherical wooden knobs were used in training and test. The entire session was filmed from the side with a digital video camera, and the training and test phases were also recorded with a webcam directed towards the infant and parent; the video from the webcam served as the primary record for coding infants' visual attention throughout the training and test phases (see Figure 1).

Procedure

Familiarization phase

The infant and caregiver sat on the floor opposite the experimenter with two sets of three toys between them, approximately 45 cm apart. The experimenter reached contralaterally for one of the toys, while saying, 'Look, [infant's name], Look!', and provided ostensive cues such as smiling, directed eye gaze, infant directed speech, and modification of the movement speed with the infant's attention. It was critical to ensure that the infant was attending to the reaching action which is why multiple ostensive cues were used (Csibra & Gergely, 2009, 2011). The experimenter reached for and manipulated the toy (e.g., rolling a wheeled toy, squeezing a sounding toy) with his contralateral hand, and then set it down and withdrew his reach before beginning another reach. He alternated between reaching with his right and left hands, switching to the other hand after performing no more than two reaches with either hand. Infants observed an average of 22.6 contralateral reaches (Ms = 11.7 and 10.9 reaches with the left and right hands, respectively), which lasted 137 s on average (SD = 20 s). Immediately following this familiarization phase, the caregiver lifted the infant onto her lap on one side of a table facing the testing apparatus and the experimenter.

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[1] We tested 9-month-old infants in order to remain consistent with previous research and to strike a balance between the emergence of the A-not-B error and contralateral reaching, which increases considerably from 6 to 12 months (Gampe et al., 2015; Melzer et al., 2012).

Figure 1. Example of an infant observing a contralateral reach during object hiding on an A-trial of the test phase.

Training phase

There were four trials with a single well following the procedure used by Longo and Bertenthal (2006). On the first trial, the toy and lid were placed on top of the box on either side of the well and the apparatus was slid forward so that the infant could grasp the toy and/or lid. On the second trial, the toy was placed in the well; on the third trial, the toy was placed in the well and was partially covered with the lid; and on the final trial, the toy was placed in the well and was completely covered by the lid. Each trial began with the lid set to one side of the well and the toy on the opposite side. The experimenter consistently grasped the toy with a contralateral reach with one hand (e.g., using his left hand when the toy was to the right of the well), and then grasped the lid with a contralateral reach with the other hand (e.g., grasping the lid to the left of the well with his right hand). No infant failed to remove the lid and grasp the toy on the final training trial. The experimenter then removed the single well apparatus, replaced it with the two-well apparatus, and administered the A and B search trials.

Test phase

The experimenter reached for the toy and rattled it to draw the infant's attention, placed it between the wells, withdrew his hand, and waited 3-s. Next, the experimenter reached for the toy, rattled it, removed the A-well lid with his ipsilateral hand, placed the toy within the well with a contralateral reach, covered it with the lid, withdrew his hands, waited 3-s, then removed the A-well lid and retrieved the toy with a contralateral reach (see Figure 1), and placed it between the wells. This sequence was repeated six times. Finally, the experimenter hid the toy in the B-well using the same hand he had used to grasp the toy on each of the A-trials, waited 3-s, and then slid the apparatus forward for the infant to search. We administered only one B-trial to prevent the possibility of carryover effects due to repeated reaches leading to a dissipation of the response bias. The right/left position of the

A-location and the hand used to perform each reach was counterbalanced across infants. With the exception of the familiarization phase, the procedure was the same as the contralateral reach condition in Longo and Bertenthal (2006) Experiment 2.

Behavioural coding

We coded whether infants searched correctly or committed the A-not-B error from the video recordings using a frame-by-frame analysis (30-frames-per-second). Two measures of visual attention were also coded: (1) looking first to the A- or B-location on the search trial, and (2) duration of looking to the A- and B-locations and to the experimenter's hands (i) during the A-trials, (ii) during the 3-s delay immediately after the toy was hidden at the B-location, and (iii) during infants' search. The minimum duration of participant looking at any specific target that was detectable was approximately 200 ms (i.e., six video frames). Also, we coded the latency to search for the toy by subtracting the video timestamp of the last frame of the box moving forward from the timestamp of the first frame that the infant touched either well lid. All coding was conducted by a trained observer unfamiliar with the hypotheses of the experiment, with looking durations on 20% of the trials coded by a second observer to establish reliability, $r(40) = .99, p < .001$.

Results and discussion

Twenty of the 30 infants (66.7%) committed the search error (see Figure 2). This rate is significantly greater than chance ($p < .05$, one-tailed binomial test). For comparison purposes, Longo and Bertenthal (2006) reported that 53.3% of the infants who observed the experimenter perform contralateral reaches during the A-trials and 86.7% of infants who observed the experimenter perform ipsilateral reaches during the A-trials committed a search error.[2]

Table 1 summarizes the looking time results during each phase of the task. There were no significant differences in looking at A or B during the A-trials for infants who committed the A-not-B error and those who searched correctly; the same is true for looking times at the experimenter's hands during the A-trials or during the delay immediately after the object was hidden at B, all $ts(28) \leq 0.88$, all $p \geq .39$. These results suggest that visual attention during the A-trials and delay cannot explain infants' search behaviour. By contrast, during the search phase, infants who committed the A-not-B search error looked more at A than infants who searched correctly, $t(28) = 5.20, p < .001$, and conversely, looked less at B, $t(28) = -5.85, p < .001$. Infants who committed the search error were also more likely than infants who searched correctly to look first at the A-location when they were given the opportunity to search, $\chi^2(1, N = 30) = 7.18, p = .007$ (see Figure 3). These findings are consistent with previous findings showing that looking and searching covaried during the B-trial (Bell & Adams, 1999; Cuevas & Bell, 2010). Finally, there was a marginally significant search latency difference between infants who committed the search error ($M = 5.1$ s) and those who searched correctly ($M = 8.9$ s), $t(28) = 1.93$, $p = .063$, which is reminiscent of a related finding that 4-year-old children's success in a perseveration task increases with increased delay (Diamond, Kirkham, & Amso, 2002).

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[2] These are the data reported in Longo and Bertenthal (2006) Experiment 2, which, except for the addition of the reach familiarization phase, was procedurally identical to the present study.
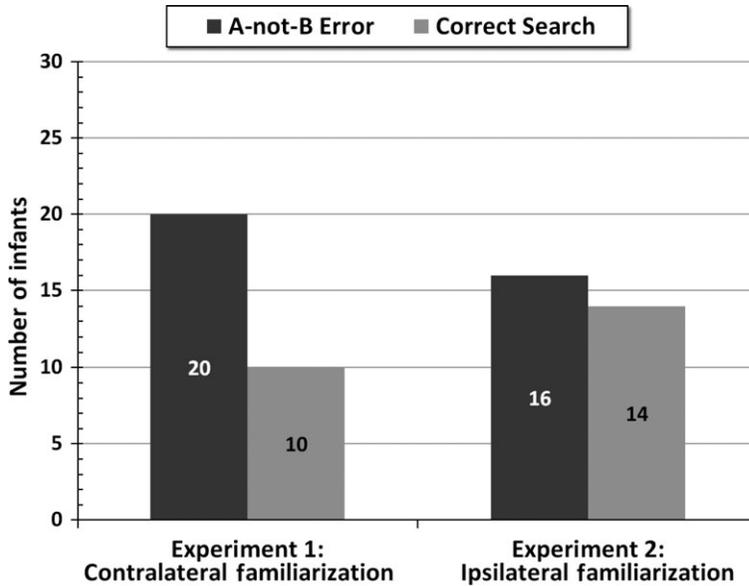
Figure 2. Number of infants who searched correctly at the B-location or searched incorrectly at the A-location in each experiment.

Table 1. Infants' looking times (in seconds) at the A- and B-locations and the experimenter's hands as a function of correct versus incorrect (A-not-B error) search on the B test trial

	Search	A-trials			Delay		Search	
		A	B	Hands	A	B	A	B
Experiment 1	Correct	36.3	5.0	45.3	1.0	1.5	0.7	5.2
	Incorrect	38.7	4.8	41.7	1.1	1.2	2.8	0.5
Experiment 2	Correct	41.2	6.3	44.6	0.6	1.6	0.5	4.5
	Incorrect	40.3	6.1	46.3	1.0	1.4	3.2	1.0

In sum, these data suggest that briefly familiarizing infants with contralateral reaching did prime their motor representations and increase the likelihood that they would map the experimenter's reaches during the A-trials to their motor representations. Visual attention during the A-trials could not explain infants' search errors, but visual attention during the B-trial did covary with search behaviour. It is also noteworthy that search errors were associated with shorter search latencies, suggesting that the motor simulation may dissipate with time, and thus decreases the likelihood of motor persistence biasing the response. A related possibility is that longer latencies might reflect greater uncertainty in the choice of where to search because the motor representation is not sufficiently activated or the memory for the object's location persists and competes with the motor bias (cf., Thelen *et al.*, 2001).

These results thus suggest that familiarizing infants with contralateral reaching prior to testing them in the A-not-B search task increased the likelihood that infants would activate a motor representation while observing the experimenter search on the A-trials. Given the design of this experiment, it could not be determined whether this was due to encoding
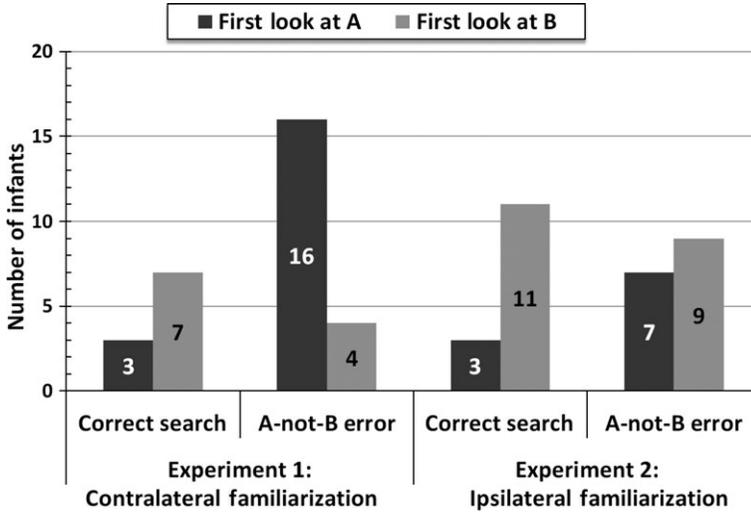
Figure 3. Number of infants who first looked at the A- or B-location as a function of search location and experiment.

the experimenter's movements or goals. If the increased likelihood of a search error was a function of encoding the goal of the reach, then it should not matter whether infants observe the experimenter reaching contralaterally or ipsilaterally during the familiarization phase. If, however, the increased likelihood of a search error was due to specifically encoding a contralateral reaching movement, then familiarizing infants with ipsilateral reaching should not increase the likelihood of their committing a search error.

EXPERIMENT 2

This experiment tested whether infants primed with ipsilateral reaching during the familiarization phase would subsequently commit the search error on an observational version of the A-not-B search task where the experimenter reaches contralaterally.

Method

Participants

Thirty 9-month-old infants participated (M = 277-days, SD = 11-days; 15 females, 15 males). An additional two infants were excluded due to simultaneously searching at both locations. Participant recruitment was the same as Experiment 1.

Materials

The materials were identical to those of the previous study.

Procedure

The procedure was identical to that of Experiment 1, except during the familiarization phase, the experimenter reached ipsilaterally. Infants observed an average of 20.5

ipsilateral reaches (10.2 and 10.3 reaches with the left and right hands, respectively), over an average of 132 s (SD = 14 s). The training and test trials proceeded exactly as in Experiment 1.

Behavioural coding

Infants' first looks and search behaviour on the B-trial as well as looking times during each phase of the experiment were coded as in Experiment 1, with looking durations on 20% of the trials coded by a second observer to establish reliability, $r(40)$ = .99, $p < .001$.

Results and discussion

Sixteen of the 30 infants (53.3%) committed the search error, which does not differ from chance ($p > .10$, binomial test). As previously noted, Longo and Bertenthal (2006, Experiment 2) reported 53.3% of infants who observed the experimenter reach contralaterally on A-trials committed the search error.

Infants who searched correctly and those who committed the A-not-B error did not differ in how long they looked at A- or B-locations, or the experimenter's hands during the A-trials or the delay after the object was hidden in the B-trial, all ts(28) $\leq$ 1.07, all $p \geq .29$. Similar to Experiment 1, during the search phase, infants who committed the search error spent more time looking at the A-location than those who searched correctly, $t(28)$ = 6.99, $p < .001$, and less time looking at the B-location, $t(28)$ = −5.10, $p < .001$. With regard to first looks on the B-trials, there was no difference between those who made the search error and those who searched correctly, $\chi^2(1, N = 30)$ = 1.67, p = .196 (see Figure 3). Also, there was no search latency difference between infants who committed the A-not-B error (M = 5.3 s) and those who searched correctly (M = 6.2 s), $t(28)$ = .81, p = .43.

Overall, these results provide no evidence that short-term visual experience with ipsilateral reaching resulted in any systematic change to infants' behaviour. Although more infants in Experiment 1 than in this experiment committed the search error, and although the proportion of infants who committed the search error in Experiment 1 exceeded chance and that for Experiment 2 did not, the number of infants committing the search error in the two experiments did not statistically differ, $\chi^2(1, N = 60)$ = 1.11, p = .29. Nevertheless, there were other differences. In comparison with infants in Experiment 1 (19/30 of whom looked at the A-location first), infants in this experiment were more likely to look to the B-location first (20/30 looked at the B-location first), $\chi^2(1, N = 60)$ = 5.41, p = .02 (see Figure 3). We further tested this difference with a logistic regression to determine whether familiarization condition (contralateral vs. ipsilateral) and infant search location (A vs. B) were significant predictors of where infants first looked. The results revealed that both familiarization condition, B = 1.20, p = .04, and manual search location, B = −1.64, p = .007, were significant predictors of first looks, and together accounted for a significant amount of variance, Nagelkerke R^2 = .27.

These results suggest that the two familiarization experiences differentially affected infants' initial direction of attention as they began to search for the hidden toy. This difference could not be attributed to differential attention on the A-trials, because infants looked at the A-location for the majority of time in both familiarization conditions. Instead, we hypothesize that where infants first looked on the B-trial was analogous to the explanation given in a goal prediction task. If infants are capable of representing the

observed action, then they shift their gaze towards the goal before the action occurs (Cannon *et al.*, 2012; Henrichs *et al.*, 2014; see Gredebäck & Falck-Ytter, in press, for a review). After observing the experimenter search for the hidden object on six trials, infants were likely to expect the experimenter to reach on the B-trial as well. If they had developed a response bias from observing the experimenter reach for the object on the A-trials, then they would have been even more likely to look at the previously correct location than to search there. The significant difference in first looks as a function of familiarization conditions thus supports the suggestion that short-term visual experience with contralateral reaching is capable of priming 9-month-old infants' motor representations.

In sum, the observation of ipsilateral reaching was not sufficient to prime the infant's motor representation for contralateral reaches during the search task as measured by their search or predictive looking behaviours. It thus appears that encoding the specific movements of the experimenters' contralateral reaches during the familiarization phase was necessary to prime contralateral reaching during the search task. In order to avoid any misunderstanding, we are not suggesting that the experimenter's goals were unimportant, but rather that familiarization with goal-directed reaching, in and of itself, was insufficient to prime the infant's motor representation for activation during subsequently observed contralateral reaches. At least for this task, it is important for infants to not only perceive the goals of the observed action, but the specific relation between the movements and goals. By analogy, researchers who study imitation distinguish between emulation (copying the effect or the goal of the action) and imitation (copying both the movement as well as the goal; Elsner, 2007). This is why we suggest that infants who committed the search error in the current experiments were 'covertly imitating' the experimenter's reaching actions.

GENERAL DISCUSSION

Recent research suggests that the actions that infants perform and their perception and understanding of those same actions are reciprocally related (e.g., Daum *et al.*, 2011; Elsner & Aschersleben, 2003; Hauf, 2007; Paulus *et al.*, 2011; Sommerville *et al.*, 2005). The results from this study contribute to this literature by suggesting that a brief familiarization with actions that are not yet well developed increases infants' likelihood of mapping these observed actions to their own motor representations. This mapping involves both the movements and the goals of the action, which explains the results of Experiment 2: Infants were familiarized with ipsilateral reaching, which was insufficient to prime their motor representation for contralateral reaching when they were tested by an experimenter who only reached contralaterally. By contrast, infants familiarized with contralateral reaching in Experiment 1 were more likely to map the observation of the experimenter's contralateral reaching during the A-trials to their motor representations, and consequently were more likely to show a response bias to the A-location on the B-trial. Taken together, these results suggest that priming a motor representation is a function of, (1) its developmental state, as well as, (2) the degree to which the immediately perceived input matches both the movements and the goals of the motor representation.

As previously discussed, contralateral reaching develops later and more slowly than ipsilateral reaching (Gampe *et al.*, 2015; Melzer *et al.*, 2012; Provine & Westerman, 1979; van Hof *et al.*, 2002). Although a significant proportion of infants showed a search error following familiarization with contralateral reaching, this proportion of the sample was

still a good deal lower than what had been previously reported for infants who observed an experimenter reaching ipsilaterally in the A-not-B search task (Longo & Bertenthal, 2006). This result makes sense in that a less developed motor representation for contralateral reaching is unlikely to achieve the same level of activation as a more developed representation, and thus, the accumulated history of activation over the A-trials will not result in as strong of a response bias. Admittedly, this was a modest effect given that there was no significant difference between the proportion of infants committing the search error in Experiments 1 (contralateral familiarization) and 2 (ipsilateral familiarization). Nevertheless, the results are bolstered by the significant differences in first looks to the A- and B- locations, which, as we previously argued, suggests that the majority of infants anticipated that the experimenter would search in the incorrect location in Experiment 1, but such anticipation was not present in Experiment 2. These visual anticipations are consistent with infants' understanding the goal of an action and follow from their mapping an observed action onto their motor representation (Gredebäck & Falck-Ytter, in press). As contralateral reaching continues to develop, we would expect that infants' likelihood of committing a search error on this task would increase because of the concomitant increase in the activation of the motor representation.

These results showing the effects of brief experiences on infants' performance converge with previous findings showing that perceptual input modifies motor representations (e.g., Legerstee & Markova, 2008; Meltzoff, 1995). As such, researchers must consider that the state of the infant during an experiment is dynamic rather than static and that learning can occur from the beginning to the end of an experiment (Bertenthal, Gredebäck, & Boyer, 2013). Even neonates show improvements in performance with repeated observations. For example, Meltzoff and Moore (1983) reported that the amplitude and accuracy of neonatal imitation increased with repeated observations of the model, thus suggesting that their motor representations change in real time with additional visual experience. More generally, infants change their focus of attention from one trial to the next, and the information encoded interacts with both their prior knowledge and their actions (Call & Carpenter, 2002). It is thus important to acknowledge that infants' motor representations and performance will sometimes change during a study as a direct consequence of the experience acquired during the testing session.

The findings from the current study also represent a challenge to recent claims that observational learning is insufficient for infants' learning about goal-directed actions. For instance, Sommerville, Hildebrand, and Crane (2008) found that 10-month-old infants' ability to identify the goal of a novel means-end task increased following active experience with the task, but not after observational experience seeing another person perform the task (see also Gerson & Woodward, 2012). By contrast, infants in Experiment 1 of the current study merely observed the experimenter perform goal-directed actions, which was sufficient to result in an above chance likelihood of showing a search error on the B-trial of the search task. In order to avoid any misunderstanding, we do not disagree that active experience is often more successful in facilitating action understanding than passive experience because, among other things, it demands greater attention to the critical features of the action (Bertenthal & Boyer, 2015; Ristic & Enns, 2015). Indeed, infants' search errors are typically higher following active than passive A-trials in the A-not-B search paradigm (Landers, 1971; Longo & Bertenthal, 2006), and it is feasible that a familiarization protocol that required infants to perform active contralateral reaches would have been even more effective than the observational familiarization procedure used here. For the current study, however, observational learning was sufficient, perhaps

because the social communicative cues used by the experimenter also increased the likelihood of infants attending to the critical information about the actions (Bertenthal & Boyer, 2015; Csibra & Gergely, 2009, 2011).

In conclusion, motor representations include both movements and goals. When infants observe others' reaching actions, they map both the movement and the goal onto their motor representation. The motor representations develop slower for contralateral than for ipsilateral reaching, but they can be primed with brief observational experiences that direct attention to critical features of the action. These features must include whether the reach is performed ipsilaterally or contralaterally, and without this matching movement information, there is no evidence that the observed action is mapped to the infant's motor representation. These findings contribute to the emerging literature on the development of action understanding by suggesting that infants' mapping observed actions to motor representations is facilitated by brief, but salient, visual experiences with these actions.

Acknowledgements

References

Barton, A. A., & Bertenthal, B. I. (2013). Infants differentially anticipate the goals of ipsilateral and contralateral reaches. *Journal of Vision*, *13*, 283. doi:10.1167/13.9.283

Bell, M. A., & Adams, S. E. (1999). Comparable performance on looking and reaching version of the A-not-B task at 8 months of age. *Infant Behavior and Development*, *22*, 221–235. doi:10.1016/S0163-6383(99)00010-7

Bertenthal, B. I., & Boyer, T. W. (2015). The development of social attention in humans. In A. Puce & B. I. Bertenthal (Eds.), *The many faces of social attention: Behavioral and neural measures*. New York, NY: Springer International Publishing AG.

Bertenthal, B. I., Gredebäck, G., & Boyer, T. W. (2013). Differential contributions of development and learning to infants' knowledge of object continuity and discontinuity. *Child Development*, *84*, 413–421. doi:10.1111/Cdev.12005

Bertenthal, B. I., & Longo, M. R. (2008). Motor knowledge and action understanding: A developmental perspective. In R. L. Klatzky, M. Behrmann & B. MacWhinney (Eds.), *Embodiment, ego-space, and action: 34th Carnegie symposium on cognition* (pp. 323–368). Mahwah, NJ: Erlbaum.

Bertenthal, B. I., & von Hofsten, C. (1998). Eye, head and trunk control: The foundation for manual development. *Neuroscience and Biobehavioral Reviews*, *22*, 515–520. doi:10.1016/S0149-7634(97)00038-9

Boyer, T. W., Pan, J. S., & Bertenthal, B. I. (2011). Infants' understanding of actions performed by mechanical devices. *Cognition*, *121*(1), 1–11. doi:10.1016/j.cognition.2011.05.012

Bruner, J. S. (1969). Eye, hand, and mind. In D. Elkind & J. H. Flavell (Eds.), *Studies in cognitive development: Essays in honor of Jean Piaget* (pp. 223–235). Oxford, UK: Oxford University Press.

Call, J., & Carpenter, M. (2002). Three sources of information in social learning. In E. Dupoux (Ed.), *Language, brain, and cognitive development* (pp. 211–228). Cambridge, MA: The MIT Press.

Cannon, E. N., Woodward, A. L., Gredebäck, G., von Hofsten, C., & Turek, C. (2012). Action production influences 12-month-old infants' attention to others' actions. *Developmental Science*, *15*, 35–42. doi:10.1111/j.1467-7687.2011.01095.x

Clearfield, M. W., Dineva, E., Smith, L. B., Diedrich, F. J., & Thelen, E. (2009). Cue salience and infant perseverative reaching: Tests of the dynamic field theory. *Developmental Science*, *12*, 26–40. doi:10.1111/j.1467-7687.2008.00769.x

Csibra, G., & Gergely, G. (2009). Natural pedagogy. *Trends in Cognitive Sciences*, *13*, 148–153. doi:10.1016/j.tics.2009.01.005

Csibra, G., & Gergely, G. (2011). Natural pedagogy as evolutionary adaptation. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *366*, 1149–1157. doi:10.1098/rstb.2010.0319

Cuevas, K., & Bell, M. A. (2010). Developmental progression of looking and reaching performance on the A-not-B task. *Developmental Psychology*, *46*, 1363–1371. doi:10.1037/a0020185

Daum, M. M., Prinz, W., & Aschersleben, G. (2009). Means-end behavior in young infants: The interplay of action perception and action production. *Infancy*, *14*, 613–640. doi:10.1080/15250000903263965

Daum, M. M., Prinz, W., & Aschersleben, G. (2011). Perception and production of object-related grasping in 6-month-olds. *Journal of Experimental Child Psychology*, *108*, 810–818. doi:10.1016/j.jecp.2010.10.003

Decety, J. (1996). Neural representations for action. *Reviews in the Neurosciences*, 7, 285–297. doi:10.1515/REVNEURO.1996.7.4.285

Decety, J., Grezes, J., Costes, N., Perani, D., Jeannerod, M., Procyk, E., & Fazio, F. (1997). Brain activity during observation of actions: Influence of action content and subject's strategy. *Brain*, *120*, 1763–1777. doi:10.1093/brain/120.10.1763

Diamond, A. (1985). Development of the ability to use recall to guide action, as indicated by infants' performance on AB. *Child Development*, *56*, 868–883. doi:10.2307/1130099

Diamond, A. (1991). Neuropsychological insights into the meaning of object concept development. In S. Carey & R. Gelman (Eds.), *The epigenesis of mind: Essays on biology and cognition* (pp. 67–110). Hillsdale, NJ: Erlbaum.

Diamond, A., Kirkham, N., & Amso, D. (2002). Conditions under which young children can hold two rules in mind and inhibit a prepotent response. *Developmental Psychology*, *38*, 352–362. doi:10.1037//0012-1649.38.3.352

Diedrich, F. J., Thelen, E., Smith, L. B., & Corbetta, D. (2000). Motor memory is a factor in infant perseverative errors. *Developmental Science*, *3*, 479–494. doi:10.1111/1467-7687.00140

Elsner, B. (2007). Infants' imitation of goal-directed actions: The role of movements and action effects. *Acta Psychologica*, *124*, 44–59. doi:10.1016/j.actpsy.2006.09.006

Elsner, B., & Aschersleben, G. (2003). Do I get what you get? Learning about the effects of self-performed and observed actions in infancy. *Consciousness and Cognition*, *12*, 732–751. doi:10.1016/S1053-8100(03)00073-4

Gampe, A., Keitel, A., & Daum, M. M. (2015). Intra-individual variability and continuity of action and perception measures in infants. *Frontiers in Psychology*, *6*, 327. doi:10.3389/fpsyg.2015.00327

Gerson, S. A., & Woodward, A. L. (2012). A claw is like my hand: Comparison supports goal analysis in infants. *Cognition*, *122*, 181–192. doi:10.1016/j.cognition.2011.10.014

Gredebäck, G., & Falck-Ytter, T. (in press). Eye movements during action observation. *Perspectives on Psychological Science*.

Greenwald, A. G. (1970). Sensory feedback mechanisms in performance control: With special reference to the ideomotor mechanism. *Psychological Review*, 77, 73–99. doi:10.1037/h0028689

Hamlin, J. K., Hallinan, E. V., & Woodward, A. L. (2008). Do as I do: 7-month-old infants selectively reproduce others' goals. *Developmental Science*, *11*, 487–494. doi:10.1111/j.1467-7687.2008.00694.x

Hauf, P. (2007). Infants' perception and production of intentional actions. In C. von Hofsten & K. Rosander (Eds.), *From action to cognition: Progress in brain research* (pp. 285–301). Amsterdam, The Netherlands: Elsevier Science.

Henrichs, I., Elsner, C., Wilkinson, N., Elsner, B., & Gredebäck, G. (2014). Goal certainty modulates infants' goal-directed gaze shifts. *Developmental Psychology*, *50*, 100–107. doi:10.1037/a0032664

Heyes, C. (2011). Automatic imitation. *Psychological Bulletin*, *137*, 463–483. doi:10.1037/a0022288

Hommel, B. (1996). The cognitive representation of action: Automatic integration of perceived action effects. *Psychological Research*, *59*, 176–186. doi:10.1007/BF00425832

Hommel, B., Musseler, J., Aschersleben, G., & Prinz, W. (2001). The theory of event coding (TEC): A framework for perception and action planning. *The Behavioral and Brain Sciences*, *24*, 849–937. doi:10.1017/S0140525X01000103

James, W. (1890). *The principles of psychololgy* (Vol. 2). New York, NY: Henry Holt.

Király, I., Jovanovic, B., Prinz, W., Aschersleben, G., & Gergely, G. (2003). The early origins of goal attribution in infancy. *Consciousness and Cognition*, *12*, 752–769. doi:10.1016/S1053-8100(03)00084-9

Landers, W. F. (1971). Effects of differential experience on infants' performance in a Piagetian Stage IV object-concept task. *Developmental Psychology*, *5*, 48–54. doi:10.1037/h0031064

Legerstee, M., & Markova, G. (2008). Variations in 10-month-old infant imitation of people and things. *Infant Behavior and Development*, *31*, 81–91. doi:10.1016/j.infbeh.2007.07.006

Lepage, J.-F., & Théoret, H. (2007). The mirror neuron system: Grasping others' actions from birth? *Developmental Science*, *10*, 513–529. doi:10.1111/j.1467-7687.2007.00631.x

Longo, M. R., & Bertenthal, B. I. (2006). Common coding of observation and execution of action in 9-month-old infants. *Infancy*, *10*, 43–59. doi:10.1207/s15327078in1001_3

Marcovitch, S., & Zelazo, P. D. (1999). The A-not-B error: Results from a logistic meta-analysis. *Child Development*, *70*, 1297–1313. doi:10.1111/1467-8624.00095

Marshall, P. J., Young, T., & Meltzoff, A. N. (2011). Neural correlates of action observation and execution in 14-month-old infants: An event-related EEG desynchronization study. *Developmental Science*, *14*, 474–480. doi:10.1111/j.1467-7687.2010.00991.x

Meltzoff, A. N. (1995). Understanding the intentions of others: Re-enactment of intended acts by 18-month-old children. *Developmental Psychology*, *31*, 838–850. doi:10.1037/0012-1649.31.5.838

Meltzoff, A. N., & Moore, M. K. (1983). Newborn infants imitate adult facial gestures. *Child Development*, *54*, 702–709. doi:10.2307/1130058

Melzer, A., Prinz, W., & Daum, M. M. (2012). Production and perception of contralateral reaching: A close link by 12 months of age. *Infant Behavior and Development*, *35*, 570–579. doi:10.1016/j.infbeh.2012.05.003

Morange, F., & Bloch, H. (1996). Lateralization of the approach movement and the prehension movement in infants from 4 to 7 months. *Early Development and Parenting*, *5*, 81–92. doi:10.1002/(SICI)1099-0917(199606)5:2 < 81:AID-EDP119 > 3.0.CO;2-M

Nishitani, N., & Hari, R. (2000). Temporal dynamics of cortical representation for action. *Proceedings of the National Academy of Science*, *97*, 913–918. doi:10.1073/pnas.97.2.913

Nystöm, P., Ljunghammar, T., Rosander, K., & von Hofsten, C. (2011). Using mu rhythm desynchronization to measure mirror neuron activity in infants. *Developmental Science*, *14*, 327–335. doi:0.1111/j.1467-7687.2010.00979.x

Paulus, M., Hunnius, S., Vissers, M., & Bekkering, H. (2011). Bridging the gap between the other and me: The functional role of motor resonance and action effects in infants' imitation. *Developmental Science*, *14*, 901–910. doi:10.1111/j.1467-7687.2011.01040.x

Piaget, J. (1937/1954). *The construction of reality in the child* (M. Cook, Trans.). New York, NY: Basic Books.

Prinz, W. (1997). Perception and action planning. *The European Journal of Cognitive Psychology*, *9*, 129–154. doi:10.1080/713752551

Provine, R. R., & Westerman, J. A. (1979). Crossing the midline: Limits of early eye-hand behavior. *Child Development*, *50*, 437–441. doi:10.2307/1129420

Rakison, D. H., & Woodward, A. L. (2008). New perspectives on the effects of action on perceptual and cognitive development. *Developmental Psychology*, *44*, 1209–1213. doi:10.1037/a0012999

Ristic, J., & Enns, J. T. (2015). The changing face of attentional development. *Current Directions in Psychological Science*, *24*, 24–31. doi:10.1177/0963721414551165

Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annual Review of Neuroscience*, *27*, 169–192. doi:10.1146/annurev.neuro.27.070203.144230

Rizzolatti, G., Fadiga, L., Gallese, V., & Fogassi, L. (1996). Premotor cortex and the recognition of motor actions. *Cognitive Brain Research*, *3*, 131–141. doi:10.1016/0926-6410(95)00038-0

Rizzolatti, G., & Sinigaglia, C. (2010). The functional role of the parieto-frontal mirror circuit: Interpretations and misinterpretations. *Nature Reviews Neuroscience*, *11*, 264–274. doi:10.1038/nrn2805

Smith, L. B., Thelen, E., Titzer, R., & McLin, D. (1999). Knowing in the context of acting: The task dynamics of the A-not-B error. *Psychological Review*, *106*, 235–260. doi:10.1037/0033-295X.106.2.235

Sommerville, J. A., Hildebrand, E. A., & Crane, C. C. (2008). Experience matters: The impact of doing versus watching on infants' subsequent perception of tool-use events. *Developmental Psychology*, *44*, 1249–1256. doi:10.1037/A0012296

Sommerville, J. A., & Woodward, A. L. (2005). Pulling out the intentional structure of action: The relation between action processing and action production in infancy. *Cognition*, *95*, 1–30. doi:10.1016/j.cognition.2003.12.004

Sommerville, J. A., Woodward, A. L., & Needham, A. (2005). Action experience alters 3-month-old infants' perception of others' actions. *Cognition*, *96*, B1–B11. doi:10.1016/j.cognition.2004.07.004

Southgate, V., Johnson, M. H., El Karoui, I., & Csibra, G. (2010). Motor system activation reveals infants' on-line prediction of others' goals. *Psychological Science*, *21*, 355–359. doi:10.1177/0956797610362058

Thelen, E., Schöner, G., Scheier, C., & Smith, L. B. (2001). The dynamics of embodiment: A field theory of infant perseverative reaching. *The Behavioral and Brain Sciences*, *24*, 1–86. doi:10.1017/S0140525X01003910

van Elk, M., van Schie, H. T., Hunnius, S., Vesper, C., & Bekkering, H. (2008). You'll never crawl alone: Neurophysiological evidence for experience-dependent motor resonance in infancy. *NeuroImage*, *43*, 808–814. doi:10.1016/j.neuroimage.2008.07.057

van Hof, P., van der Kamp, J., & Savelsbergh, G. J. P. (2002). The relation of unimanual and bimanual reaching to crossing the midline. *Child Development*, *73*, 1353–1362. doi:10.1111/1467-8624.00476

Wellman, H. M., Cross, D., & Bartsch, K. (1986). Infant search and object permanence: A meta-analysis of the A-not-B error. *Monographs of the Society for Research in Child Development*, *51*, 1–51. doi:10.2307/1166103

Woodward, A. L. (1998). Infants selectively encode the goal object of an actor's reach. *Cognition*, *69*, 1–34. doi:10.1016/S0010-0277(98)00058-4

Woodward, A. L., & Gerson, S. A. (2014). Mirroring and the development of action understanding. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *369*, 20130181. doi:10.1098/rstb.2013.0181

Zelazo, P. D., Reznick, J. S., & Spinazzola, J. (1998). Representational flexibility and response control in a multistep multilocation search task. *Developmental Psychology*, *34*, 203–214. doi:10.1037/0012-1649.34.2.203