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RESEARCH ARTICLE

The development of grasping comprehension in infancy: covert shifts of attention caused by referential actions

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Abstract An eye tracking paradigm was used to investigate how infants' attention is modulated by observed goal-directed manual grasping actions. In Experiment 1, we presented 3-, 5-, and 7-month-old infants with a static picture of a grasping hand, followed by a target appearing at a location either congruent or incongruent with the grasping direction of the hand. The latency of infants gaze shift from the hand to the target was recorded and compared between congruent and incongruent trials. Results demonstrate a congruency effect from 5 months of age. A second experiment illustrated that the congruency effect of Experiment 1 does not extend to a visually similar mechanical claw (instead of the grasping hand). Together these two experiments describe the onset of covert attention shifts in response to manual actions and relate these findings to the onset of manual grasping.

Keywords Infancy · Goal-directed actions · Action perception · Grasping action · Saccadic reaction times · Eye tracking

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Introduction

In the present study, we used a spatial cueing paradigm to investigate infants' comprehension of manual grasping actions. Using an eye tracking paradigm, we measured saccadic reaction times of infants as they shift their attention from a still picture of a grasping hand to a subsequently presented peripheral target.

Manual grasping is one of the most important action skills used in our everyday life. Grasping is used for exploration and for reshaping our environment via manipulation (Flanagan and Johansson 2002). Newborn infants already aim their extended arm movements towards interesting objects (von Hofsten 1982). However, intentional reaching and successful grasping towards static or slowly moving objects emerges a few months later, at the age of 3–4 months (von Hofsten and Lindhagen 1979). These early grasping skills rapidly improve. At 5–6 months, grasping has become proficient enough that infants extrapolate object motions on the linear paths well ahead in time (von Hofsten et al. 1998; Hespos et al. 2009). Nine-month-olds adjust their hand aperture relative to the size of the target object (von Hofsten and Rönnqvist 1988) and 1-year-olds develop pincer grasps (e.g., Johnson and Blasco 1997). As in adults, infants' grasping movements are predictive (von Hofsten 2004) and, as such, oriented towards the future location of objects within an ever-changing environment.

Within the first year of life, infants also develop a remarkable sensitivity to the goal of others' grasping actions (e.g., Woodward 1998). In Woodward's seminal study, infants were habituated to a grasping action towards one of two objects. In a subsequent test phase in which the positions of the two objects were switched, 6-month-old infants demonstrated a stronger novelty response to the hand grasping a new object (while maintaining the old motion path) than for the hand grasping the same object in a new position. It is thus apparent that 6-month-olds form an expectation about the actor's goal. Six-month-old infants also encode the goal of uncompleted grasping actions (Daum et al. 2008; Hamlin et al. 2008) and infer the size of a goal object from the aperture size of the actor's hand during the grasp (Daum et al. 2009).

Over the next few months, infants' ability to encode the goal of others' reaching actions becomes increasingly sophisticated. At 1 year of age, infants are able to infer goals from a variety of socially relevant cues like gaze direction (Woodward 2003), emotional expressions (Phillips et al. 2002), and pointing (Woodward and Guajardo 2002; Tomasello et al. 2007). At this age, infants are also able to infer the goal of an action performed not only by a human agent but also by a mechanical claw (Woodward 1998; Hofer et al. 2005). All of the above-mentioned action comprehension studies investigate infants' tendency to react to a change that occurs from an initial set of habituation trials to a subsequent set of test trials. During this process, an expectation about the action is compared to the actual outcome of the action upon completion of the observed action.

In addition to making such post hoc *evaluations*, young infants also *anticipate* the goal of others' actions online. These studies often rely on eye tracking technology to measure the location of infants' gaze (or overt shifts of attention) as they view manual actions being performed by others. Recent research with 14-month-old infants has shown that anticipatory gaze shifts depend on the future intention of an observed reaching action, and that infants fixate the goal of functional reaching actions earlier than the end-point of moving, non-functional closed fists (Gredebäck et al. 2009). However, infants' ability to anticipate the goal of others' actions is not isolated to reaching or grasping actions. In fact, 12-month-olds are able to anticipate the goal of manual displacement actions directed towards a container (Falck-Ytter et al. 2006) and manual feeding actions directed towards someone else's mouth (Gredebäck and Melinder 2010) whereas 6-month-olds anticipate the goal when observing an actor feeding herself (Kochukhova and Gredebäck, in press).

The studies described above suggest that infants develop both manual capabilities and action comprehension abilities (as measured by both anticipation and retrospective evaluations) within their first year of life. With the present study, we intended to take our understanding of infants' comprehension of grasping actions one step further, going beyond this previous research by focusing on the following three aspects. First, most of the studies focusing on infants' action comprehension involved visible goals (see Legerstee et al. 2000, for exceptions; Daum et al. 2009). To fully comprehend grasping actions, it is however necessary for an observer to predict the location of a goal from observing the grasping hand per se. One major goal of the present study was thus to test infants' comprehension of the directionality of a grasping hand with no goal object being present simultaneously with the grasp.

A second and related question of the present study was whether and when infants are able to infer the directionality of a grasping action from the still picture of a grasping hand during the grasp, thus not entailing any actual motion information. It is known from studies with adult participants that photographs of scenes that include implied motion activate the same higher-order visual brain areas (e.g., medial temporal cortex, medial superior temporal cortex, or superior temporal sulcus) as during the perception of real motion (Kourtzi and Kanwisher 2000; Senior et al. 2000; Peuskens et al. 2005). More importantly, extrapolation of motion information about observed actions induces selective activation of the motor cortex (Urgesi et al. 2006), and this activation is strongest during the perception of ongoing but incomplete actions (Urgesi et al. 2010). However, it is not known whether similar inferential processing is already in place in infants at an age when they start to perform grasping actions.

Third, and most importantly, little is known about when the direction of a grasp is coded and how long it takes from the presentation of a grasping hand until attention is shifted in the direction of the grasping hand. Thus, we are interested in the processing timeline of infants' action understanding and the involved processes that precede post hoc evaluations and observable shifts of overt attention (i.e., anticipations), in this case shifts of covert attention.

Overt and covert shifts of attention are usually thought to be linked by a common underlying mechanism (Rizzolatti et al. 1987; Moore and Fallah 2001). It is assumed that shifts of covert attention precede shifts of overt attention in order to scan the environment for interesting objects or locations. Upon detection of such an object or location, an eye movement is triggered towards this location (Wright and Ward 2008). Based on this assumption, we hypothesized that a similar mechanism is involved during the observation of a grasping action early in infancy. That is, while observing a grasping hand, the attention of an observer is first shifted covertly in the direction of the grasping action and then, upon detection of a goal object, followed by an eye movement towards the goal. Accordingly, the second main goal of the present study was to measure shifts of infants' covert attention during the observation of a grasping hand.

The fact that humans can direct their attention towards an area without explicitly looking at this location has been extensively investigated by Michael Posner (1978, 1980). He demonstrated that adults' reaction times for detecting a peripheral target can be influenced by a directional cue, for example an arrow, preceding the target. If this cue was followed by a target that appeared at a location congruent with the direction of the cue, the reaction time was faster than if the target appeared at the opposite location, incongruent with the direction of the cue. Similar to adults, 4-month-old infants can learn the relationship between arbitrary central cues and peripheral targets and adjust their covert attention accordingly (Johnson et al. 1991).

This priming effect has also been demonstrated in response to the direction of another's gaze in both adults (Friesen and Kingstone 1998; Driver et al. 1999; Ricciardelli et al. 2000; Langdon and Smith 2005) and infants (Hood et al. 1998). In the study by Hood et al. (1998), 3-month-old infants were presented with a female face who shifted her gaze to the side. This was followed by a peripheral target, appearing at a location either congruent or incongruent with the gaze shift. In accordance with the general priming literature, infants attended to the same location as the eyes of the perceived face, as indicated by the latency and the direction of their orientation (Hood et al. 1998). This research has shown that infants at a very young age already are able to predict the referent of an observed gaze shift from the action itself, without the referent or goal being present during the observation of the gaze shift. To our knowledge, no studies have investigated infants' covert shifts of attention with respect to manual grasping actions. Given the fact that (a) infants are able to shift their covert attention based on observed gaze shifts (e.g., Hood et al. 1998) and (b) infants at early age are able to attribute goals to a reaching agent in their post hoc evaluations (Woodward 1998) and anticipate goals of observed manual actions (Kochukhova and Gredebäck, in press), we suggest that the development of attention modulation by social cues is paramount. Focusing further on modulation of covert attention by human grasping actions will further extend our understanding of how infants perceive and encode manual actions, and enhance our knowledge about the mechanisms that mediate the development of action comprehension in general. Accordingly, we relied on an eye tracking paradigm to measure the saccadic reaction time of 3-, 5-, and 7-month-old infants as they attended to a central cue (grasping hand) and shifted their attention to the reappearance of a peripheral target. By comparing reaction times to congruent (target appeared along the linear extension of the grasping hand) and incongruent trials (target appeared in the opposite direction), we were able to investigate the presence of covert attention shifts during the observation of manual reaching actions. Due to the fact that congruent and incongruent trials were presented with equal probabilities, the presentation of the grasping hand per se was non-predictive. Differences in reactive saccade latencies have therefore to be based on the perception and comprehension of the directionality of the observed grasping hand. We hypothesized that infants develop the ability to shift their covert attention in the direction of another's grasping actions at the same time as they develop their own manual grasping abilities. More specifically, we predict that infants will develop the first signs of covert attention shifts (as measured by faster saccadic latencies to congruent than incongruent trials) between 3 and 5 months of age. This prediction is based on the rapid development of manual grasping ability that occurs over the same time period (von Hofsten and Lindhagen 1979).

Experiment 1

In Experiment 1, infants' ability to shift attention based on the perception of a goal-directed grasping action was investigated using a spatial priming paradigm (Hood et al. 1998). Following a central attention grabber, a grasping hand (cue) was presented, followed by a peripheral object (target) that was located at a position congruent or incongruent with the grasping direction. Infants' reaction times (time before infants fixated the target) were assessed with eye tracking technology.

Method

Participants

The final sample consisted of eighteen 3-month-olds (8 girls, 10 boys; mean age: 3 months; 5 days, range: 2;24–3;15), eighteen 5-month-olds (8 girls, 10 boys; mean age: 5;4, range: 4;28–5;13) and eighteen 7-month-olds (8 girls, 10 boys; mean age: 6;29, range: 6;15–7;13). Nineteen additional 3-month-olds (16 girls, 3 boys) were tested but not included in the final sample due to distress or fussiness ($n = 3$), poor calibration ($n = 10$), fewer than 6 valid trials ($n = 5$), or mean reaction times of 3 SD above the overall mean ($n = 1$). Seven additional 5-month-olds (2 girls, 4 boys) were tested but not included in the final sample due to poor calibration ($n = 3$) or fewer than 6 valid trials ($n = 4$). Four additional 7-month-olds (3 girls, 1 boy) were tested but not included in the final sample due to poor calibration ($n = 1$), fewer than 6 valid trials ($n = 2$), or mean reaction times of 3 SD above the overall mean ($n = 1$). The large number of infants excluded due to poor calibration is caused by the fact that especially the 3-month-olds[1] often got inattentive during the calibration

[1] The large number of infants that were not included in the final analysis is not unusual for research with infants at the age of 3 months (e.g., Luo and Baillargeon 2005; Sommerville et al. 2005; Wang et al. 2005).

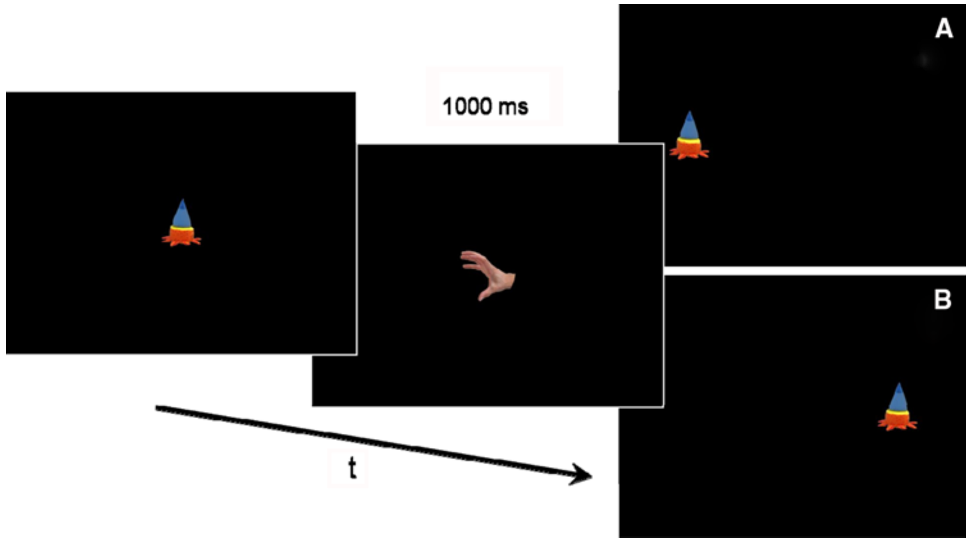

Fig. 1 Stimulus sequence for each trial in Experiment 1. (1) Attention grabber (looming at 1 Hz with sound) presented until the infants fixated it, then the trial is started. (2) Cueing hand is presented for 1,000 ms. (3) Target (same as attention grabber, looming with 1 Hz with sound) appears at an either congruent (**a**) or incongruent (**b**) location

sequence, what resulted in poor calibration quality. The data had therefore to be excluded from further analysis. Contact information for the infants was obtained from public birth records.

Test environment, stimuli and apparatus

The laboratory was unfurnished except for the test equipment. The 5- and 7-month-old infants were seated in a car safety seat (Maxi Cosi Cabrio), which was placed in front of the eye tracker. The 3-month-olds were seated on one parent's lap. The stimuli were presented, and gaze was measured using a Tobii 1750 near infrared eye tracker with an infant add-on (precision: 1°, accuracy: 0.5°, sampling rate: 50 Hz). A 9-point infant calibration was used. During calibration, a blue and white sphere expanded and contracted (extended diameter = 3.3 visual degrees) in synchrony with a sound. Viewing distance was approximately 60 cm.

Each trial started with a looming stimulus (Fig. 1), either a multicoloured wooden tower, a yellow rubber duck, a multicoloured soft textile cube, or a multicoloured soft textile cone (horizontal and vertical dimensions: maximum 4.5°, minimum 2.3°) presented at the centre of the monitor (24.8 × 20.7°) and accompanied by a brief attention-grabbing sound. As soon as the infant fixated the central stimulus, a hand (cue) was presented grasping in one of four directions (to the right, left, up, or down, 5.0 × 4.6°) for 1,000 ms. The presentation of the grasping hand was followed by a renewed presentation of the initial stimulus (now referred to as the target). The target appeared at a location that was either congruent with the grasping hand (in the same direction as the grasping hand, see Fig. 1a) or incongruent (in the opposite direction to the grasping hand, i.e., left when the hand cued to the right, above when the hand was directed downwards and vice versa, see Fig. 1b). The distance from the nearest edge of the hand to the target was 9.3°. The target remained visible until the infant looked at it for approximately 1,000 ms or until 5,000 ms had elapsed. Then, a new trial began with the centrally presented looming stimuli.

The order of the targets as well as the relation between the grasping hand and the location of the target was randomized. Congruent and incongruent trials were presented at equal probabilities. In order to avoid adaptation effects to the direction of the grasping hand, we counterbalanced the overall grasping direction (horizontal vs. vertical) on every other trial. This ensured that the latency of target-oriented gaze shifts on any given trial was not influenced by the location of the target on the previous trial. The maximum number of trials presented was 64.

Procedure

Infants were tested in the laboratory at a time of day when they were likely to be alert and in good mood. All infants were tested individually with one parent present. Each participant and his/her parents were first escorted to a reception room. For approximately 10 min, the infant was allowed to explore the room while the research assistant described the test procedure to the parents, and one of the parents signed a consent form. The infant and one parent were then brought to the test room. The research assistant helped the parent to position the infant in the car seat. During stimulus presentation, the parent sat on a chair behind the infant with the car seat on his/her lap. Parents were instructed not to interact with their children during testing. They were encouraged, however, to put both hands symmetrically close to the child if it appeared necessary to comfort the infant. Once the infant and the parent seemed comfortable, the research assistant left the room, and the stimulus presentation was started.

Data analysis

For the analysis of gaze, five square areas of interest (AOI) were defined on the screen. The cue AOI covered the cueing hand (horizontal and vertical dimension: 7.5°), whereas the target AOIs covered each of the targets (horizontal and vertical dimension: 4.7°). A trial was considered to be valid if the infant fixated the central cue for at least 200 ms (Gredebäck et al. 2006) prior to making a gaze shift to the target. The saccadic reaction time (SRT) was defined as the reaction time between the appearance of the target and the arrival of the infant's gaze in the respective target AOI (Gredebäck et al. 2010a). Individual reaction times of less than 100 ms and more than 3 standard deviations of each individual mean were excluded from analysis. Infants had to produce a minimum number of six trials to be included in the final analysis. *P*-values are reported two-tailed throughout.

The analyses were performed in three steps: (1) an overall analysis of variance on SRTs with congruency and direction (horizontal vs. vertical) as within-subjects factors and age and sex as between-subjects factor was followed by (2) separate ANOVAs (planned comparisons) for each age group. The age-specific analysis included congruency and direction as within-subject variables. (3) Additionally, the number of infants who shifted their gaze faster towards the congruent target was compared to the number of infants who shifted their gaze faster to the incongruent target separately for each age using non-parametric Sign tests.

Results

The average number of trials was 16.6 (SD = 10.3, range: 6–44) for the 3-month-olds, 29.4 (SD = 13.8, range: 11–54) for the 5-month-olds, and 25.7 (SD = 13.7, range: 10–59) for the 7-month-olds. The overall ANOVA demonstrates significant effects of direction, $F(1, 48) = 6.75$, $P = .012$, $\eta^2 = .12$, and age, $F(2, 48) = 4.83$, $P = .012$, $\eta^2 = .17$. Mean SRTs were faster for horizontal cue target relations and decreased with increasing age (Table 1). No overall differences were observed for congruency or gender. To further explore the data, separate analyses were performed for each age group.

The 7-month-olds shifted their gaze faster from the central cueing hand to a congruent target than to an incongruent target. In addition, they tended to show shorter SRTs when the stimuli were presented horizontally ($M = 600$ ms, SD = 244 ms) than when they were presented vertically ($M = 758$ ms, SD = 358 ms). Planned

Table 1 Experiment 1: Mean saccadic reaction times in ms per age group and relation between the direction of the cueing stimulus and the location of the target

Age group	Congruent target		Incongruent target	
	Mean	SD	Mean	SD
3-month-olds	961.54	279.84	918.28	176.30
5-month-olds	815.01	299.17	908.51	458.68
7-month-olds	615.74	140.67	698.27	208.19

comparisons analysis of the SRTs of the 7-month-old infants yielded a significant effect of congruency, $F(1, 17) = 13.88$, $P = .002$, $\eta^2 = .45$, and a marginal effect of direction, $F(1, 17) = 3.79$, $P = .068$, $\eta^2 = .18$. The interaction of the two factors was not significant, $F(1, 17) = 1.08$, $P = .31$, $\eta^2 = .06$. A Sign test ($P = .001$) confirmed this finding; 16 infants shifted their gaze faster towards the congruent target, and only 2 infants did the opposite.

The analysis of the SRTs of the 5-month-old infants yielded no significant main effect or interaction (all Fs < 2.35, all ps > .14). However, the pattern of the SRTs and mean differences between SRTs during congruent and incongruent trials was comparable to the difference in the 7-month-olds; the mean difference in the SRTs between congruent and incongruent trials was 83 ms for the 7-month-olds and 94 ms for the 5-month-olds. An important difference was that the 5-month-olds' overall standard deviation (341.41 ms) was greater than the 7-month-olds' (168.20 ms), $F = 4.87$, $P = .034$ (Levene's test for equality of variances). In fact, the Sign test ($P = .031$) demonstrated a significant effect; 14 infants shifted their gaze faster towards the congruent targets, while only 4 infants did the opposite.

The analysis of the SRTs of the 3-month-old infants yielded only a significant main effect of direction, $F(1, 17) = 4.71$, $P = .045$, $\eta^2 = .22$. SRTs were shorter when the stimuli were presented horizontally ($M = 818$ ms, SD = 240 ms) than when they were presented vertically ($M = 1{,}021$ ms, SD = 395). The Sign test ($P = 1.0$) showed no significant difference; 9 infants shifted their gaze faster towards the congruent targets, while 9 infants did the opposite.

Discussion

The results of Experiment 1 demonstrate a remarkable development in infants' ability to shift their covert attention along the linear extension of a grasping hand from 3 to 7 months of age. The 7-month-olds showed a reliable and robust congruency effect. They shifted their gaze faster towards congruent than incongruent targets.

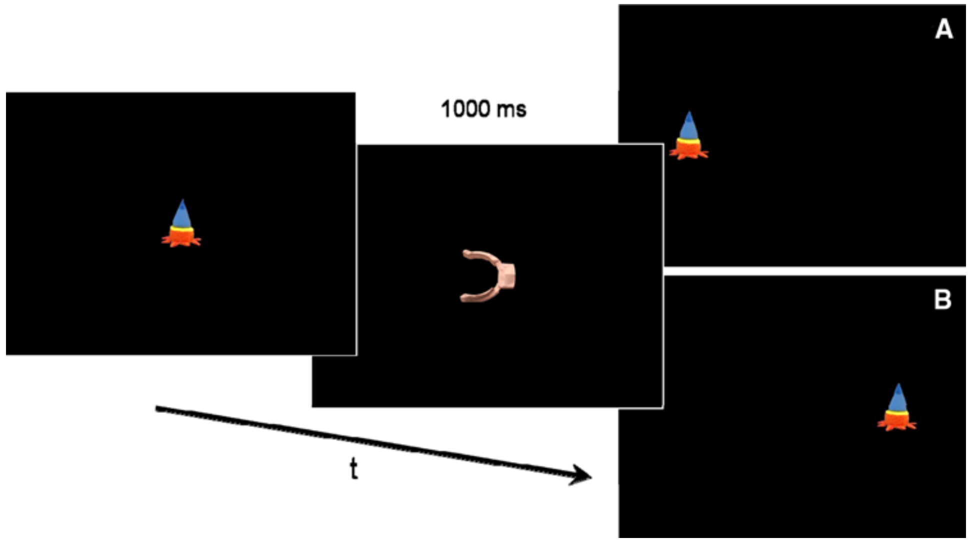

Fig. 2 Stimulus sequence for each trial in Experiment 2. (1) Attention grabber (looming at 1 Hz with sound) presented until the infants fixated it, then the trial is started. (2) Cueing hand is presented for 1,000 ms. (3) Target (same as attention grabber, looming with 1 Hz with sound) appears at an either congruent (**a**) or incongruent (**b**) location

The 5-month-olds demonstrated a reliable congruency effect only in a non-parametric analysis, showing that significantly more infants produced faster gaze shifts towards congruent than incongruent targets. Finally, the 3-month-olds did not show any differences between congruent and incongruent trials.

Based on these findings, we conclude that beginning around the age of 5 months, at a similar age when they develop their own grasping abilities, infants are able to process the direction of a perceived grasping hand and shift their covert attention accordingly.

A question that remains unanswered by Experiment 1, however, is whether the congruency effect found is specific for observed human grasping actions or whether it can be extended to other grasping actions as performed for example by mechanical devices (e.g., a grasping mechanical claw) that have similar visual properties as the hand presented in Experiment 1. We know from research with adults that the processing of grasping actions is not restricted to human actions but also accounts for robot actions (Gazzola et al. 2007). However, action processing seems to not be equally efficient for human and robotic actions. In fact, actions are processed more easily the more similar the performing agent is to oneself (e.g., Grèzes et al. 2004), and imitation of grasping actions is more strongly elicited when the action is performed by a human hand compared to a mechanical claw (Press et al. 2005).

Research with infants has shown that comprehension of goal-directed grasping actions performed by a mechanical claw starts much later than when the same action is performed by a human hand. Infants do not appear to encode the goal of mechanical claws until they are between 9 (Hofer et al. 2005; Boyer et al. 2009) and 12 months of age (Woodward 1998; Hofer et al. 2005).

Experiment 2

Consequently, in Experiment 2, 3-, 5-, and 7-month-old infants were presented with the same paradigm used in Experiment 1, except that a grasping mechanical claw (Fig. 2) replaced the grasping hand. The appearance of the grasping claw was made visually compatible to that of the grasping hand used in Experiment 1. The claw had multiple extensions on the grasping side and was covered with tan-coloured tape.

If infants' covert attention shifts are based on a general system for action comprehension (i.e., sensitive to a wide variety of actors), similar priming effects demonstrated in Experiment 1 should be present in response to the mechanical claw. If, on the other hand, infants' covert attention is modulated by a more specialized system for action comprehension (i.e., primarily sensitive to human hands), no effects of congruency should be present in any of the three age groups.

Method

Participants

The final sample consisted of eighteen 3-month-olds (8 girls, 10 boys; mean age: 3 months; 4 days, range: 2;25–3;13), eighteen 5-month-olds (12 girls, 6 boys; mean age: 5;8, range: 4;28–5;15) and eighteen 7-month-olds (8 girls, 10 boys; mean age: 7;00, range: 6;17–7;13). Eighteen additional 3-month-olds (14 girls, 4 boys) were tested but not included in the final sample due to distress or fussiness ($n = 4$), poor calibration ($n = 8$), or there being fewer than 6 valid trials ($n = 6$). Fourteen additional 5-month-olds (10 girls, 4 boys) were tested but not included in the final sample due to poor calibration ($n = 6$), providing fewer than 6 valid trials ($n = 6$), or mean reaction times 3 SD above the overall mean (n = 2). Five additional 7-month-olds (3 girls, 2 boys) were tested but not included in the final sample due to distress or fussiness ($n = 1$), poor calibration ($n = 2$), fewer than 6 valid trials ($n = 1$), or mean reaction times 3 SD above the overall mean ($n = 1$).

Apparatus, procedure and data analysis

The same apparatus was used to generate the stimulus display as in Experiment 1 except for one modification. Instead of the picture of a grasping hand, a picture of a grasping claw the same size as the hand was presented. The claw was wrapped with skin-coloured adhesive tape in order to make the visual properties as similar to the human hand used in Experiment 1 as possible. The data were analysed in the same way as in Experiment 1.

Results

The average number of trials equalled 15.6 (SD = 9.3, range: 6–48) for the 3-month-olds, 27.1 (SD = 11.6, range: 11–57) for the 5-month-olds, and 28.4 (SD = 15.6, range: 8–60) for the 7-month-olds. An overall analysis of variance on the overall reaction times yielded significant effects of direction, $F(1, 48) = 12.17$, $P = .001$, $\eta^2 = .20$, age, $F(2, 48) = 7.53$, $P = .001$, $\eta^2 = .24$, and an interaction of direction and age, $F(2, 48) = 4.80$, $P = .013$, $\eta^2 = .17$. Mean SRTs and standard deviations are shown in Table 2. Post hoc comparisons revealed that differences in the SRTs between horizontal and vertical cue-target relations were only significant in 3-month-olds, $t(17) = 2.91$, $P = .01$, and 5-month-olds, $t(17) = 2.87$, $P = .01$, but not in 7-month-olds, $t(17) = .39$, $P = .70$. Separate analyses of each age group follow below.

The analysis of the SRTs of the 7-month-old infants yielded no significant effects (all Fs < 1). The Sign test showed no significant difference; 8 infants shifted their gaze faster towards the congruent targets, while 10 infants did the opposite, $P = .82$. Five-month-old infants produced faster horizontal ($M = 633$ ms, SD = 249 ms) than vertical saccades ($M = 805$ ms, SD = 330 ms), $F(1, 17) = 8.23$, $P = .01$, $\eta^2 = .33$. However, no difference was found between congruent and incongruent trials. The sign test likewise showed no significant difference; 10 infants shifted their gaze faster towards the congruent targets while 8 infants did the opposite, $P = .82$. In a similar manner, 3-month-olds also produced faster horizontal ($M = 818$ ms, SD = 299 ms) than vertical ($M = 1{,}061$ ms, SD = 502 ms) saccades, $F(1, 17) = 8.48$, $P = .01$, $\eta^2 = .33$. No significant effect of congruency was observed, and the Sign test demonstrated no significant differences (8 infants shifted their gaze faster towards the congruent targets, while 10 infants did the opposite, $P = .82$).

Table 2 Experiment 2: Mean saccadic reaction times in ms per age group and relation between the direction of the cueing stimulus and the location of the target

Age group	Congruent target		Incongruent target	
	Mean	SD	Mean	SD
3-month-olds	950.82	331.18	930.45	331.94
5-month-olds	724.00	248.60	718.60	243.48
7-month-olds	624.95	140.22	629.24	178.80

Discussion

In Experiment 2, we tested whether the congruency effect found in Experiment 1 was based on specific comprehension of human grasping actions or whether it could be extended to similar (non-human) grasping actions. The results revealed no congruency effect for either age group. This finding fits with previous studies showing that early comprehension of grasping is highly dependent on the presence of a human actor (Woodward 1998; Hofer et al. 2005). It suggests that young infants shift their covert attention exclusively, or at least most effectively, during observation of human actions, and supports the notion that early action comprehension is more specifically tuned to human actions.

Based on Experiment 1 alone, it is conceivable that SRTs might be influenced by differences in the weight of attention awarded to the congruent grasping side and the incongruent arm extension (e.g., the number of extensions or fingers is larger on the grasping side). The claw used in Experiment 2 suggests that this was not the case. The claw had the same general spatial layout as the human hand. Despite this, the effect did not transfer to the mechanical claw. SRTs were only faster to congruent human grasping compared to incongruent human grasping.

General discussion

In the present study, infants' comprehension of grasping actions was investigated. In two experiments, we tested how and when infants' covert attention is modulated by the direction of a grasping hand compared to a grasping mechanical claw. In Experiment 1, 5-month-old infants shifted their gaze faster towards a target that appeared at a location congruent with the direction of the previously presented grasping hand compared to a target appearing in the opposite, and incongruent, location. No similar congruency effect was found in Experiment 2, where the cueing stimulus was a grasping mechanical claw. With the results of the present study, we show for the first time that young infants' covert attention is modulated by the direction of others' grasping actions. This effect exists in the absence of motion, suggesting that young infants can extrapolate the direction of a reaching action from the configuration of a static hand.

Previous research investigating modulation of infants' attention has shown that, at the age of 4 months, infants can learn the relationship between an arbitrary central cue and the peripheral target, and move their eyes more often to a cued compared to a non-cued location (Johnson et al. 1991). Infants aged 3 months have been further shown to attend to the same location as the eyes of a perceived face (Hood et al. 1998). Given the early onset of infants' ability to shift covert attention, the question might be raised why the younger infants in the present study did not yet show an effect of modulation of attention. There are two main reasons for this difference. First, in the study by Johnson et al. (1991), the infants were taught the relation of an arbitrary cue and a target. In the present study, no learning phase was provided. In fact, infants were presented with grasping hands that were non-predictive from the very first trial. Second, infants are sensitive to human eyes very early. Even newborn infants prefer direct gaze to averted gaze (Farroni et al. 2002), and they already have a rudimentary ability to follow another's gaze (Farroni et al. 2004). This is far earlier than any reported age at which infants start to intentionally produce goal-directed grasping movements and start to comprehend others' grasping actions.

The present findings can be interpreted to point towards a discrepancy between the processing of gaze and manual grasping. While infants shift their covert attention in the direction of observed gaze shifts around the age of 3 months (Hood et al. 1998), they attribute goals to observed gaze shifts much later, around 9–12 months of age (Woodward 2003; Johnson et al. 2007). In contrast, the present findings show that with respect to observed grasping actions, the onset of covert attention shifts corresponds with the onset of goal attribution during (e.g., Woodward 1998). The present findings do not fully explain the different timing patterns of the two phenomena. But one of the reasons for this discrepancy might lie in the proximity of the target object with respect to the action cue. With respect to covert attention shifts, infants infer the directionality of the cue being directed towards a *distal* target irrespective the cue being a grasping hand or a gaze shift. With respect to goal attribution, the target is *proximal* in the case of an observed grasping hand and *distal* in the case of an observed gaze shift. This difference in proximity and a related potential increase in difficulty of comprehension might serve as one reason for the delayed development of goal attribution compared to covert attention shifts in the case of observed gaze shifts compared to grasping actions. In any case, more research is needed that directly compare sensitivity to (and comprehension of) manual grasping and other referential actions (such as pointing and gaze shifts) relate to each other throughout development.

The aim of the present study was to focus on two aspects of infants' comprehension of grasping actions, the ability to infer the directionality of a grasping action from the perception of a grasping hand and the involvement of shifts of covert attention as the first step during the perception of a grasping action. With respect to these major aims, we are able to draw the following conclusions. First, the present findings show that infants are able to infer the directionality of a grasping action from the hand without the presence of a goal object being necessary and without any information about the goal location being provided. This extends findings reported in previous studies showing that infants at 6 months are able to encode the goal of an object-directed but uncompleted reaching action (Daum et al. 2008) even if the goal object is occluded during the observation of the reaching movement (Daum et al. 2009).

Second, our results show that infants are additionally able to infer the directionality of a grasping action from a still picture of a grasping hand being presented. This finding is in line with studies testing adult participants that showed that the motor system is involved during the perception of snapshots of ongoing but uncompleted actions similar to the stimulus material presented in the present study (Urgesi et al. 2006, 2010). It seems that the surface properties of the hand are sufficient to modulate infants' covert attention without the presence of any additional motion information that are intrinsic parts of all actions.

Third, this is the first study to directly demonstrate that covert attention is involved in infants' observation of others' goal-directed manual actions. This supports the idea of a processing timeline of action comprehension that starts with a shift of covert attention during the observation of the acting agent, in this case the grasping hand, in perceived direction of the grasping action. This shift of covert attention facilitates the detection of a goal object or location which then triggers the shift of overt attention via an observable eye movement. Finally, upon completion of the action, previously built expectations can be compared to the outcome of the action.

The present study provides first evidence for the timing of the processing of an observed action, demonstrating a development in the latency of gaze shifts from the hand to the target over the months investigated. In fact, saccadic reaction times decreased from about 900 ms at 3 months to 600 ms at 7 months of age. The processing time of the

7-month-olds might be compared to the temporal dynamics of neural correlates (ERP) recorded during observation of congruent and incongruent pointing gestures at 8 months of age (Gredebäck et al. 2010b). This study demonstrated a differential activity over posterior temporal areas (P400) that relates to the congruency of hand gestures (younger infants were not investigated). We acknowledge that direct comparisons between behavioural data and ERP data are difficult. At the same time, the emergence of a neural differentiation between congruent and incongruent hand gestures 400 ms after onset of the hand and the presence of a overt gaze shift 600 ms after stimulus onset in 7–8-month-old infants is intriguing.

It is, in this respect, also worth mentioning that the present study replicates and extends the literature devoted to mapping out the development of the oculomotor system. First of all, we replicate the general finding that saccadic SRTs decrease with increased age (e.g., Bronson 1982; Canfield et al. 1997; Gredebäck et al. 2006). This finding is consistent with the claim of a general increase in processing speed across development (e.g., Kail 1991). Second, SRTs were faster for horizontally than vertically presented cue-target relations. This finding is again in line with previous studies showing that infants' visual tracking of vertically moving objects is inferior to the visual tracking of horizontally moving targets (Grönqvist et al. 2006) and that SRTs are slower for vertical than for horizontal saccades (Gredebäck et al. 2006).

However, our findings differ from those of previous studies with respect to temporal aspects of the SRTs. In the present study, overall, we found longer SRTs than some previous studies (Canfield et al. 1997; Reznick et al. 2000; Gredebäck et al. 2006) that focus on oculomotor development and do not include much social information. At the same time, our results are comparable to those obtained by Hood and colleagues (Hood et al. 1998), who also used a spatial congruency paradigm to investigate how covert attention shifts are modulated by observed gaze shifts (reporting SRTs from 693 to 900 ms in 3-month-olds). The prolonged SRTs might reflect an enhanced processing of the social content of the presented central cue compared to the presentation of simple sequences of primarily non-social stimuli.

With respect to experience dependency, this study harmonizes with prior studies that demonstrate an experience dependency with respect to the ability to encode the goal of others actions (Woodward 1998; Kochukhova and Gredebäck, in press). Similar to the onset of young infants' ability to make retrospective evaluations of others' actions and their ability to anticipate the goal of an observed action online, the onset of covert attention shifts coincides with the onset of functional reaching behaviour in infancy (as described in the Introduction).

In line with previous studies (Sommerville and Woodward 2005; Falck-Ytter et al. 2006; Gredebäck and Melinder 2010), this finding provides further evidence that a very close relationship between performance and comprehension of goal-directed grasping actions is present in early infancy. In adults, this close link between action perception and production is extensively described in the theoretical framework of the common coding principle (Prinz 1990, 1997). This account assumes a bidirectional influence of action and perception, where perceived events can have an impact on planned and executed actions (Stürmer et al. 2000; Brass et al. 2001) and planned or executed action can also have an impact on the perception of events (e.g., Hamilton et al. 2004; Repp and Knoblich 2007). Further accounts like the direct matching hypothesis (Flanagan and Johansson 2003) suggest that action comprehension results from a mechanism that maps an observed action onto the observer's motor representations of that action. Explanatory evidence for underlying neural mechanisms of such a mapping system comes from research on the mirror neuron system, showing that action observation triggers a motor simulation of the observed action (for an overview, see Rizzolatti and Craighero 2004). Recently, studies exploring the desynchronization of the mu rhythm using EEG (Nyström 2008; van Elk et al. 2008) have provided evidence of an early presence of a mirror neuron system in infants. We believe that similar processes are involved in guiding covert attention shifts during observation of others actions.

An alternative explanation of why infants demonstrate a priming effect to human hands but not mechanical claws might be based on infants' prior visual experience. In line with others (Premack 1990; Leslie 1994, 1995), Biro and Leslie (2007) proposed a cue-based bootstrapping model as describing the theoretical origin of infants' interpretation of goal-directed actions. Their model suggests that the understanding of a goal-directed action can be based on pre-wired interpretative schemas triggered by distinct action-related cues such as equifinality, self-propelledness of the agent, and the presence of action effects. In order to infer the directionality of a cue, the infants might be required to identify the cue. When perceiving a hand, the identification might lead to the expectation that open hands usually move towards a to-be-grasped target. Based on the assumption of cue-based bootstrapping, one could argue that infants in the present study might have inferred the directionality not primarily based on their experience in producing grasping actions but rather on their experience in observing the respective grasping cues. In the case of the human hand, infants might then have accumulated quite an amount of experience during the first month due to the observation of their parents and siblings grasping for objects, in the case of the mechanical claw, in contrast, infants might have accumulated less knowledge regarding the claw as an agent. We would like to emphasize, however, that in the present study, the infants did not receive any information about action-related cues such as equifinality, self-propelledness of the agent, or action effects. The infants were presented with the picture a disembodied human hand or a mechanical claw grasping in one of four directions. The hand was then replaced by the peripheral target. The hand never touched or interacted with the target, the hand did not move, and no action effects were presented. Due to the lack of availability of these cues that are necessary for interpreting observed actions as goal-directed based on pre-wired interpretative schemas (e.g., Biro and Leslie 2007), we favour the interpretation that in the present study, the modulation of covert attention during the observation of a grasping hand is to a significant extent based on the infants' own experience in performing grasping actions. To which extent prior observational experience plays a key role in the modulation of infants' covert attention is a question for further research. In order to disentangle, the contribution of prior experience and manual proficiency training studies within the current priming paradigm are necessary, investigating whether a sensitivity to the directionality of mechanical claws can be trained or not.

To conclude, the results of the present study go beyond recent findings showing that beginning at the age of 6 months, infants are able to interpret grasping actions as goal-directed. Our data provide evidence of the emergence of covert shifts of attention as one important mechanism underlying the comprehension of an observed grasping action. This implies that infants, from 5 months of age, are able to infer the goal-directedness of an observed grasping hand. This functional interpretation of a grasping gesture results in the shift of the infants' covert attention away from an actor's hand towards an actor's goal. The onset of these covert attention shifts occurs earlier in development than the onset of overt attention shifts towards to goal of a grasping action. Shifting covert attention based on the perception of a human grasping action might therefore form the bedrock of infants' comprehension of others' actions and reflects one of the milestones in infants' social-cognitive development.

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