Belief-based action prediction in preverbal infants

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ABSTRACT

Successful mindreading entails both the ability to think about what others know or believe, and to use this knowledge to generate predictions about how mental states will influence behavior. While previous studies have demonstrated that young infants are sensitive to others' mental states, there continues to be much debate concerning how to characterize early theory of mind abilities. In the current study, we asked whether 6-month-old infants appreciate the causal role that beliefs play in action. Specifically, we tested whether infants generate action predictions that are appropriate given an agent's current belief. We exploited a novel, neural indication of action prediction: motor cortex activation as measured by sensorimotor alpha suppression, to ask whether infants would generate differential predictions depending on an agent's belief. After first verifying our paradigm and measure with a group of adult participants, we found that when an agent had a false belief that a ball was in the box, motor activity indicated that infants predicted she would reach for the box, but when the agent had a false belief that a ball was not in the box, infants did not predict that she would act. In both cases, infants based their predictions on what the agent, rather than the infant, believed to be the case, suggesting that by 6 months of age, infants can exploit their sensitivity to other minds for action prediction.

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1. Introduction

Accurately predicting what others will do is mediated by our understanding that their actions are driven, not necessarily by what *we* think or know to be the case, but by what *they* think and believe. Despite being fundamental for successful social interaction, the ability to generate action predictions on the basis of others' perspectives has long been thought to be a protracted developmental achievement (Wellman, Cross, & Watson, 2001). Successful action prediction will often require at least three different stages of computation. First, one needs to understand that others' actions are goal-directed and identify what goal is motivating their behavior (e.g. she wants to get the ball). They then need to consider what that person knows or believes about their goal (e.g. she thinks her ball is in the cupboard). Finally, they need to use their representations of the other's goals and beliefs to generate a prediction about how these elements will influence her subsequent behavior (Dennett, 1989) (e.g. she will search for her ball in the cupboard).

In recent years, this view of theory of mind acquisition as progressing through stages over the first few years of life has been challenged by the discovery that, even in the first year after birth, infants not only readily interpret others' actions as goal-directed (Gergely, Nadasdy, Csibra, & Biro, 1995; Woodward, 1998), but appear to appreciate that goal-directed behavior is modulated by an agent's belief (Luo, 2011). When presented with scenarios in which an agent acts either consistently or inconsistently with how their past experience should lead them to act, preverbal infants respond with increased attention to the inconsistently-behaving agent (Onishi & Baillargeon, 2005; Surian,

Caldi, & Sperber, 2007). Furthermore, even infants as young as 7 months appear to spontaneously encode events from other's perspectives, reacting with increased interest when a ball which an agent should believe to be present is revealed to be absent (Kovacs, Teglas, & Endress, 2010).

These studies suggest that infants are sensitive to others' perspectives and resulting beliefs (Rakoczy, 2012). However, there is much debate concerning to what extent this demonstrated sensitivity to others' beliefs should be interpreted as a genuine understanding of belief. Recent theoretical papers have highlighted the various ways in which the underlying cognitive states that drive infant's behavior on non-verbal false belief tasks might fall short of a true understanding of belief (Apperly & Butterfill, 2011; Rakoczy, 2012). For example, Rakoczy (2012) discusses the possibility that infants may be relying on sub-doxastic states rather than propositional attitudes when reacting to the outcomes of events in looking-time paradigms. One essential difference is whether or not such mental states can be inferentially integrated. According to Rakoczy, a true understanding of belief requires that one appreciate that a belief is related to other mental states (e.g. goals), and to outputs (e.g. actions). It is the integration of different states (e.g. goals and beliefs) and an appreciation of the consequences of these states for action, that is central to Dennett's so-called 'Intentional Stance' which he proposes we adopt when explaining and predicting the behavior of others (Dennett, 1989). However, while an appreciation of the relationship between beliefs and other mental states, or beliefs and action, seems central to the concept of belief, we do not know whether young infants have an appreciation of these relationships. For example, in Kovacs and colleagues study, belief sensitivity manifested as interference: infants own representation of the location of a hidden object seemed to be influenced by what they knew of the others' representation of the object (Kovacs et al., 2010). While studies with young infants clearly provide evidence that infants are sensitive to others' mental states (Rakoczy, 2012), they do not provide evidence that infants understand, for example, that beliefs play a causal role in action because they do not show that infants expect that a particular belief will lead to a particular action outcome. This is, in part, because looking-time provides only an indication that infants are sensitive to some event, and cannot provide evidence that infants expected that a particular outcome would result from that event (Haith, 1998; Wellman, 2011). There is much contradictory evidence concerning the extent to which infants might understand the relationship between mental states and subsequent behavior. For example, some have suggested that infants' early sensitivity to others' goals does not support a prediction concerning how these goals will influence action (Daum, Attig, Gunawan, Prinz, & Gredebäck, 2012), whereas other evidence suggests that infants can generate predictions concerning what others will do given a particular goal, at around the same time as they demonstrate this understanding in their looking-time response (Southgate & Begus, 2013; Southgate, Johnson, El Karoui, & Csibra, 2010).

In the current study, we sought evidence that, at around the same age as infants demonstrate a sensitivity to others' beliefs (Kovacs et al., 2010), they also appreciate the causal role that beliefs play in action. Specifically, we asked whether 6-month-old infants generate action predictions that are appropriate given a false belief held by an agent. Two approaches to measuring action predictions in preverbal infants have been used in recent years. Firstly, eye tracking has revealed that infants make saccades towards the end point of an ongoing event, suggesting that they are able to generate predictions concerning how the event will culminate. For example, when infants see a hand reaching towards a previously chosen and unchosen object, they make anticipatory saccades in the direction of the previously chosen object, presumably because they predict that the hand will again approach the same object (Cannon & Woodward, 2012). While eye tracking is an extremely useful measure of action prediction, it may also have its limitations. For example, in order to demonstrate their ability to generate action predictions, infants need to disengage from a moving stimuli (e.g. a hand) and move their eyes towards a static one (e.g. an object that the hand is approaching). This ability to visually disengage from an interesting stimulus, thought to reflect endogenous attention control, continues to improve across the first year of life, with infants at 7 months being slower to disengage than infants at 14 months (Elsabbagh et al., 2013). Thus, while an absence of anticipatory saccades is commonly interpreted as an inability to generate predictions (Cannon & Woodward, 2012; Falck-Ytter, Gredeback, & Hofsten, 2006; Kanakogi & Itakura, 2011), it might also reflect infant's immature visual disengagement. An alternative approach to measuring action prediction in infancy thus relies not on eye movements, but on a likely neural correlate of action prediction, motor cortex activation. It is well known that areas of an observer's motor system are recruited when generating predictions about others' actions (Cross, Stadler, Parkinson, Schütz-Bosbach, & Prinz, 2011; Kilner, Vargas, Duval, Blakemore, & Sirigu, 2004; Schubotz, 2007; Stadler et al., 2012), and this phenomenon has also been demonstrated in infants (Southgate & Begus, 2013; Southgate, Johnson, Osborne, & Csibra, 2009; Southgate et al., 2010;). One measure of motor activation is a decrease in the resting-state alpha rhythm, recordable on the EEG, over sensorimotor cortex (Marshall & Meltzoff, 2011). For example, 9-month-old infants exhibit a significant decrease in alpha amplitude over sensorimotor cortex (implying motor activation) when they are presented with an image of an object that experience has taught them implies an impending action (Southgate & Begus, 2013), demonstrating that motor cortex activation can serve as a useful correlate of action prediction in infants. That motor cortex activation may be a more sensitive measure of infants abilities to generate action predictions is suggested by the fact that, despite not generating anticipatory eye movements towards the target object of a mechanical claw (Cannon & Woodward, 2012), even younger infants nevertheless exhibit motor activation when they observe a claw in the presence of an object that it had previously approached (but not when the claw is in the presence of an object that it had previously ignored)(Southgate & Begus, 2013).

Here, we measured motor activation to investigate whether infants would appropriately predict when

someone with a false belief will and will not reach for a box that they falsely believe either does, or does not, contain a desired object. Rather than asking where someone with a false belief will search as is typical with older children (Wimmer & Perner, 1983), measuring motor activation allows us to ask simply whether infants expect that the agent will act at all. To this end, we designed two false belief scenarios that generated different action predictions. In one case, an agent falsely believes a ball to be in a box in front of her (she was absent when the ball rolled away) and so, if infants understand that she has a false belief about the situation, and the consequences of this false belief for her subsequent action, they should predict that she will reach for the box. In the second case, the same agent falsely believes that the ball is *not* in the box (she was absent when the ball returned). If the infant understands that she has a false belief, and the consequences of this belief for her action, they should not expect that she will reach for the box. These two conditions make opposing predictions about activity in the motor system. In the case where the agent falsely believes the ball to be present (herein called the A+O− condition, where the agent believes the ball to be present but the observer knows the ball to be absent), an expectation of action should lead to an increase in motor activation, as measured by a decrease in sensorimotor alpha suppression. In the case where the agent falsely believes the ball to be absent (herein called the A−O+ condition, where the agent believes the ball to be absent but the observer knows the ball to be present), no expectation of action should result in no increase in motor activation and no decrease in sensorimotor alpha suppression.

In Experiment 1, we first verified our measure and design with a group of adult participants. In Experiment 2, we tested a group of 6-month-old infants.

2. Experiment 1

In Experiment 1, we tested a group of adult participants in order to confirm that our neural measure of action prediction yielded the expected results. Adults were presented with two kinds of false belief trials in which either the agent had a false belief that a desired ball was inside a box in front of her, or she had a false belief that the ball was not inside the box. Although her belief was false in both cases (since the observing adult knew that the ball was actually not inside the box, or was inside the box, respectively), the observer's expectation that the agent would act should differ depending on the agent's belief. In the case where the agent falsely believes the ball to be in the box (A+O), the observer should expect that she would reach for the box to obtain the ball. As action predictions are accompanied by motor activation, we expected to see evidence of motor activation on A+O− trials. However, in the case where the agent has a false belief that the ball is not in the box (A−O+), the observer should not expect her to act towards the box and we should not see evidence of motor activation in the observer. Such differential motor activation would indicate that the observer is indeed interpreting the events as intended and appreciates the consequences of false beliefs for subsequent actions. The

second aim of testing adults was to simultaneously obtain eye-tracking data to provide support for our use of motor activation as a measure of action prediction. In previous studies, it has been shown that motor activation accompanies action predictions, and is absent when an action is not expected, in both adults (Kilner et al., 2004) and infants (Southgate & Begus, 2013). Here we hypothesize that participants will exhibit motor activation when they predict that the agent will reach for the box. If observers are indeed expecting the agent to reach for the box, they might be expected to focus more on the agent's hand when they expect her to reach than when they do not expect her to reach. Thus, we analyzed not only whether observer's exhibited more motor activation on A+O− trials than A−O+ trials, but also whether they generated more eye-movements towards the agent's hand on A+O− trials than on A−O+ trials.

2.1. Methods

2.1.1. Participants

11 undergraduate students contributed to the final sample of data. A further 16 participants were tested but excluded from the final sample. Primarily, despite instructing participants to avoid blinking, the long length of trials made this difficult and 14 participants blinked during the anticipation period of most trials and so, as with previous studies investigating motor activation in adults (Babiloni et al., 2009; Streltsova, Berchio, Gallese, & Umilta, 2010), their data was excluded. The data of 2 additional adults was excluded because of excessive noise (1) and technical problems (1). Participants received course credit or monetary compensation for participation.

2.1.2. Stimuli

Stimuli consisted of two types of 14 s trials. The two types of test trial began with the ball either rolling towards and jumping into the box from the right-hand side of the screen (A+O− trials) or jumping out of the box and rolling away to the right-hand side of the screen (A−O+ trials). After this initial event, a curtain came down to hide the agent. At this point, the box opened again and the ball either jumped out of the box and rolled away (A+O− trials) or rolled towards and jumped into the box (A−O+ trials). In both trial types, the lid then closed and the curtain was raised to reveal the actress stationary and looking downward at the closed box (see Fig. 2 for the same sequence of events in the format presented to infants. The image in Fig. 1 depicts the slightly different arrangement presented to adults). The actress then behaved consistently with her false belief. In A+O− trials, she remained stationary for 1500 ms before reaching towards and grasping the lid of the box (1500 ms). In A−O+ trials, she remained stationary for 3000 ms to equate the length of the two trials. Test trials were presented in a pseudo-randomized order and were presented on a 58×10^2 cm screen. To keep the adult and infant version comparable, participants were presented with no more than 20 repetitions of each trial type. After artefact rejection, included adults contributed between 8 and 13 (median = 10) A+O− trials, and between 6 and 13 (median = 9) A−O+ trials. There was no significant
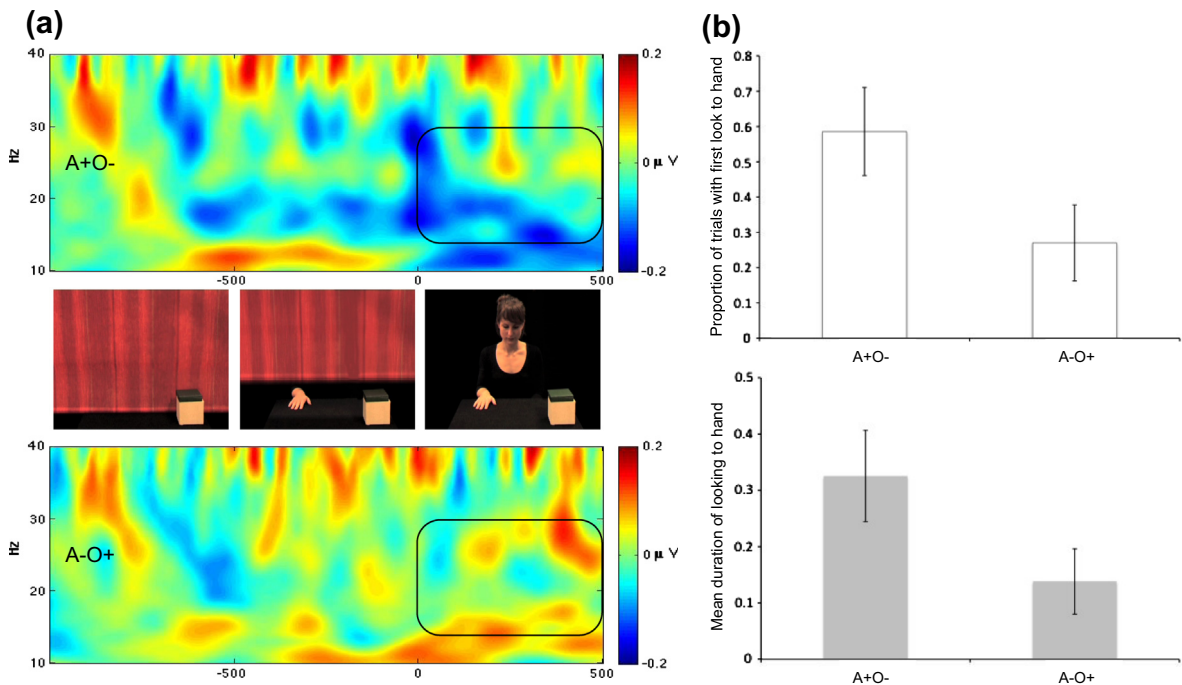
(a)

(b)

Fig. 1. Adult participant results. (a) EEG data: time–frequency (TF) plots for the 2 types of test trial. TF plots reflect baseline corrected activity averaged over the four left sensorimotor channels, and over all participants. Zero is the onset of the agent reappearance and activity averaged over the first 500 ms of this period was compared to the baseline period. Black rectangles indicate the time and frequency range over which statistics were computed. (b) Eye-tracking data: upper graph shows the proportion of valid trials on which the participant's first anticipation was directed towards the agent's hand on the two types of false belief trial, and lower graph shows the mean duration of participant's looking to the agent's hand on the two types of false belief trial.
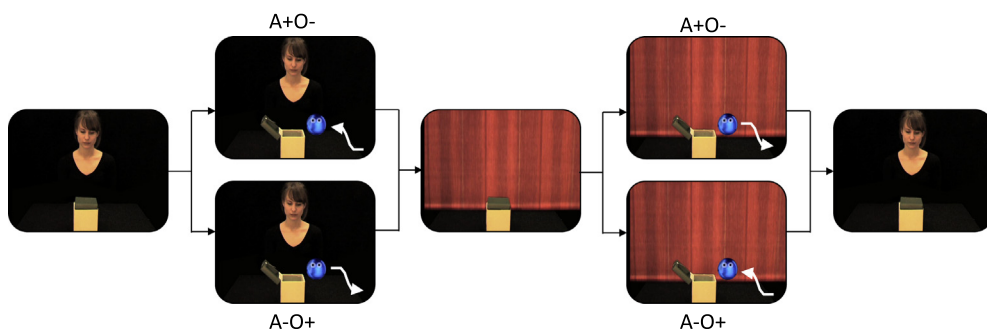

Fig. 2. The two types of false belief test trial presented to infants. Each began with either the ball jumping into the box (A+O−) or jumping out of the box (A−O+). The actress then disappeared behind a curtain and infant watched as the ball then jumped out of the box (A+O−), or jumped back in (A−O+). The curtain then rose to reveal the actress, stationary, looking down at the box. Changes in sensorimotor alpha were measured during this stationary reappearance period.

difference in the number of trials contributed between the two trial types ($p > .4$).

2.1.3. Procedure

2.1.3.1. EEG. EEG was recorded continuously using a 128-electrode Hydrocel Geodesic Sensor Net (Electrical Geodesic, Eugene, USA), sampled at 250 Hz, recorded with respect to the vertex electrode and re-referenced to the average prior to analysis. Following recording, EEG was segmented into 5500 ms segments (beginning 3500 ms before, and ending 2000 ms after, the point at which the

agent reappeared) and time–frequency analyses were performed on each artefact-free segment by continuous wavelet transform using Morelet wavelets at 1 Hz intervals in the 6–30 Hz range. To eliminate distortion created by the wavelet transform, the first and last 500 ms of each segment was removed. A 400 ms period, beginning 1000 ms before the reappearance of the actress, was selected as a baseline. This time window was chosen as the event occurring within it, the onset of the curtain raising to reveal the actress, was the same in both test trial types. Averaged activity in the baseline period was subtracted from the first

500 ms following the agent's reappearance, during which the agent was stationary. Average wavelet coefficients within participants were calculated by taking the mean across trials. Based on previous research indicating the presence of motor activation in the beta band (13–30 Hz) in adults (Caetano, Jousmäki, & Hari, 2007; Kilner, Marchant, & Frith, 2009), we analyzed activity across this entire frequency range. Unlike for infants, we had no strong prediction concerning whether motor activation should be lateralized and so we analyzed activity at both left and right sensorimotor electrodes (left: 30, 36, 37, 42; right: 87, 93, 104, 105).

2.1.3.2. Eye tracking. Throughout EEG data acquisition, eye-tracking data was also obtained. A Tobii (Stockholm, Sweden) TX300 Eye Tracker was used in standalone mode and with a sampling rate of 300 Hz. Eye-tracking data was collected and synchronized with EEG data via custom-built Matlab scripts, employing the T2T package (http://psy.ck.sissa.it/t2t/About_T2T.html). Prior to the beginning of the experiment, a 5-point calibration was carried out.

2.2. Results

2.2.1. EEG

Average activity in the 13–30 Hz range was compared in a $2 \times 2 \times 2$ ANOVA with Time (Baseline vs. agent reappearance), Trial type (A+O− vs. A−O+), and Location (Left vs. Right electrodes) as within-subjects factors. This analysis revealed a significant interaction between Time and Trial type [$F(1, 10) = 13.69$, $p = .004$, $\eta_p^2 = .578$] and a main effect of Location that approached significance [$F(10) = 3.56$, $p = .08$, $\eta_p^2 = .263$]. Consequently, we decided to analyze amplitude at each location separately. A 2 (Time) × 2 (Trial type) ANOVA on left hemisphere channels revealed a significant interaction between factors. Follow-up paired-samples *t*-tests on each Trial Type separately showed that there was a significant decrease in amplitude from baseline to the agent reappearance for A+O− trials [$t(10) = 2.82$, $p = .02$] but no decrease from baseline to agent reappearance for A−O+ trials [$t(10) = -1.25$, $p = .24$]. The same ANOVA on right hemisphere channels did not reveal any significant effects [p's > .1]. This result implies that adults recruited their motor cortex on A+O− trials, when the agent with the false belief that the object is present should be expected to reach for the box, but not on the A−O+ trials, when the agent with the false belief that the object is absent should not be expected to reach for the box. As with previous research in infants, this effect was restricted to left sensorimotor cortex. The presence of motor activation when the agent had a false belief about the ball's presence, but not when she had a false belief about the ball's absence, suggests that participants made a different prediction about what she would do in each case. Specifically, the presence of motor activation, which has previously been demonstrated when adults and infants expect someone else to act (Caetano et al., 2007; Kilner et al., 2004; Southgate & Begus, 2013), in the A+O− condition, suggests that participants expected the agent to reach for the box and based their action prediction on what the agent, rather than the infant, believed to be the case.

2.2.2. Eye tracking

To add support to our interpretation that motor activation reflects a prediction that the agent will act in the A+O− condition, but that she will not act in the A−O+ condition, we analyzed participant's eye-movements during this anticipation period, reasoning that if they were indeed predicting an action in one condition but not the other, that they may also generate overt fixations towards the hand in the A+O− condition but not in the A−O+ condition. Visual inspection suggested that participants fixated 3 regions during the anticipatory period: they remained fixated on the agent's face, they shifted their gaze to the agent's hand, or they shifted their gaze to the box in front of the agent. Participants were equally likely to shift their gaze from the agent's face on both A+O− and the A−O+ trials (median = 8 trials for A+O− and 9 trials for A−O+ trials, a difference that is not significant, $p = .4$). Thus, we asked whether, out of those trials on which participants did shift their gaze during the anticipatory period (valid trials), whether they were more likely to shift their gaze to the hand on A+O− trials than on A−O+ trials. To address this question, we took two measures. First, we asked whether participants were more likely to make a first look to the hand on A+O− trials than on A−O+ trials. To account for the fact that participants did not make an anticipatory look on every trial,[1] we divided the number of trials on which participants made a first look to the hand by the total number of valid trials (47 % of all presented trials). This analysis showed that participants made significantly more first looks to the hand on A+O− trials than on A−O+ trials [59% of all first looks were to the hand on A+O− trials, compared to only 27% on A−O+ trials, $t = (10) = 2.74$, $p = .02$], a finding that was also confirmed with non-parametric statistics [$Z = -2.1004$, $p = .04$, two-tailed]. For our second measure, we asked whether participants spent longer fixating the hand in the A+O− condition than in the A−O+ condition. To do this, we calculated the total duration of fixations towards the hand on each trial and again divided this number by the number of trials contributing this data. This analysis revealed that participants spent longer fixating the hand in the A+O− condition than in the A−O+ condition [$t(10) = 2.53$, $p = .03$], a result again confirmed with non-parametric statistics [$Z = -2.31$, $p = .02$, two-tailed]. Together, these analyses demonstrate that on trials in which participants should expect the agent to act if they have taken into account her false belief (the A+O− trials), they are more likely to fixate on her hand first, and spend more time fixating on her hand, than on trials in which they should not expect her to act (A−O+ trials). Together with previous research which has implicated the motor system in action prediction (Caetano et al., 2007; Kilner et al., 2004; Schubotz, 2007; Southgate & Begus, 2013; Southgate et al., 2009), the tendency to fixate the agent's hand during the anticipation period on A+O− trials, when participants also exhibit a significant increase in motor activation, supports our interpretation that the motor activation we see on these trials does reflect the participant's prediction that the agent will act.

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[1] This was either because the eye tracker lost the participant's eyes during the anticipatory period or because the participant did not shift their eyes from the agent's face.

3. Experiment 2

In Experiment 2, we used our EEG measure to ask whether 6-month-olds predict others' actions in accord with their belief states. Previous research has shown that infants of around the same age are indeed sensitive to others' beliefs (Kovacs et al., 2010), but it is unknown whether infants of this age have any appreciation of the functional consequences of those beliefs. The experiment was identical to that run with adults with 2 exceptions. First, infants were given 4 familiarization trials to familiarize them with the agent's goal (to obtain the ball) and the 2 different outcomes (agent reaches, agent does not reach). Furthermore, since we only measured EEG with infants,[2] we reduced the likelihood of infants making large horizontal eye movements during the anticipatory period by positioning the box directly in front of the agent and her hand behind the box (see Fig. 2).

3.1. Methods

3.1.1. Participants

13. full-term 6-month-olds participated in the study (mean age 185 days; range 173–204 days). To be included in the analysis, infants were required to provide at least 6 artefact- and movement-free trials for each of the two test trial types. An additional 21 infants were excluded from the analysis because they contributed too few artefact- and movement-free trials (17), had extreme amplitude values ($z > 2.5$) (1), or because of experimenter and/or equipment error (3). The final number of infants included and the exclusion rate is typical of EEG studies with infants (Marshall, Young, & Meltzoff, 2010; Saby, Marshall, & Meltzoff, 2012; Southgate, Csibra, Kaufman, & Johnson, 2008; Stapel, Hunnius, van Elk, & Bekkering, 2010).

3.1.2. Stimuli

Stimuli consisted of four 7 s familiarization trials and the same two types of 14 s test trials that were presented to adults. Familiarization trials were included to familiarize infants with the agent's goal and with both the reach and no reach outcomes, and the outcomes (reach or no reach) were always consistent with the agent's experience (i.e. she reached when the ball had jumped into the box but she did not reach when the ball had jumped out of the box and left the scene). Both familiarization trials began with an actress seated in front of a small box, the lid of which then opened. In the first familiarization, a blue ball rolled from the right-hand side of the screen and jumped into the box, after which the lid closed and the actress reached towards the box. In the second familiarization, the same ball jumped out of the box, rolled away to the right of the screen, after which the lid closed and the actress remained looking at the box but without reaching.

With the exception that, for infants, the box was placed directly in front of the agent, the two types of test trial (Fig. 2) were identical to those presented to adult partici-

pants. Test trials were presented in a pseudo-randomized order with the stipulation that within every 10 trials, 5 repetitions of each test trial type should be presented to ensure that we could collect enough data given the limited amount of trials infants were likely to tolerate.

3.1.3. Procedure

Four familiarization trials (2 of each kind) were followed by repeated presentations of the two types of test trial until infants became inattentive. The procedure for EEG was the same as described for adults. Unlike for adults, the frequency band that appears to be most reactive during action execution in infants is the alpha band (Southgate & Begus, 2013; Southgate et al., 2009; Southgate et al., 2010). In previous studies with 9-month-old infants, we obtained reaches from infants and identified their individual frequency range (Southgate & Begus, 2013; Southgate et al., 2009; Southgate et al., 2010). However, obtaining clear reaches from 6-month-old infants was often difficult,[3] and so rather than select the alpha frequency band to be analyzed on the basis of participant's own reaching, we averaged all infant's data over the 5–7 Hz frequency band, which encompasses the alpha frequency band in infants of this age (Berchicci et al., 2011; Marshall, Bar-Haim, & Fox, 2002). Thus, 5–7 Hz averaged activity in the baseline period was subtracted from the first 500 ms following the actress' reappearance, during which the actress was stationary. Average wavelet coefficients within infants were calculated by taking the mean across trials. Based on previous work showing that, in infants, motor activation during action prediction is restricted to the left sensorimotor cortex (Southgate & Begus, 2013; Southgate et al., 2009; Southgate et al., 2010), we analyzed activity over the cluster of 4 left sensorimotor channels (electrode numbers 30, 36, 37 and 42). As in infants we expect to find evidence of motor activation within the alpha frequency, we additionally analyzed changes within the alpha band at 4 occipital channels (electrode numbers 70, 71, 76 and 83, approximating O1 and O2 on the 10–10 layout) in order to ensure that any central alpha changes are not confused with occipital alpha changes. Reported analyses reflect data averaged over each cluster of 4 electrodes.

3.2. Results

Average amplitude in the 5–7 Hz frequency range was compared in a 2×2 ANOVA with Time (Baseline vs. Actress reappearance) and Trial type (A+O− vs. A−O+) as within-subjects factors, and revealed a significant interaction between these two factors [$F(1,12) = 7.01$, $p = .02$, $\eta_p^2 = .37$]. Follow-up paired-samples t-tests were carried out on each condition separately. For the A+O− condition, there was a significant decrease in alpha amplitude from baseline to the point of agent reappearance [$t(12) = 2.31$, $p = .04$], indicating motor cortex activation when the agent, who had a false belief that the ball was in the box, returned to the scene. On the other hand, there was a

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non-significant *increase* in alpha amplitude from baseline in the A−O+ condition, where the agent had a false belief that the ball was not in the box [$t(12) = 1.51$, $p = .16$] (Fig. 3). The presence of motor activation when the agent had a false belief about the ball's presence, but not when she had a false belief about the ball's absence, suggests that infants made a different prediction about what she would do in each case. Specifically, the presence of motor activation, which has previously been demonstrated when an observer expects someone else to act (Caetano et al., 2007; Kilner et al., 2004; Southgate & Begus, 2013), in the A+O− condition, suggests that infants expected the agent to reach for the box and based their action prediction on what the agent, rather than the infant, believed to be the case. Furthermore, to ensure that our left sensorimotor effect in the A+O− condition reflects changes in the sensorimotor alpha rhythm, and not the more posterior occipital alpha rhythm, we analyzed changes in a cluster of occipital channels where previous studies have shown the visual alpha rhythm to be dominant (Stroganova, Orekhova, & Posikera, 1999). A repeated measures ANOVA with Time and Condition revealed no significant main effects nor interactions [p's > .5], confirming that our effect is a central, motor, phenomenon. Finally, a non-parametric test confirmed that our results are representative of the group. 10 out of 13 infants exhibited a decrease in alpha amplitude from baseline (indicating motor activation) to agent reappearance on A+O− trials, whereas only 4 out of 13 infants exhibited such a decrease on A−O+ trials. A Fisher's exact test confirmed that this difference is significant ($p = .047$, two-tailed).

As our paradigm was an EEG paradigm, infants were presented with multiple presentations of the two test videos. Infants contributed a median total of 8 A+O− trials (range = 6–12) and 7 A−O+ trials (range = 6–12). It is possible that infants therefore learned during the experiment which outcome – reach or no reach – went with which video sequence, and our results reflect a learned association. To address this question, we separately analyzed valid trials that infants contributed from the first half of the experiment (i.e. artefact and movement-free trials occurring during the first 50% of the total trials the infant viewed, median 3 A+O− (range = 2–5) trials and 4 A−O+(range = 3–5 trials)) and valid trials from the second half of the experiment (median 4 A+O− (range = 3–5) trials and 3 A−O+(range = 2–5) trials). A repeated measures ANOVA with Time and Condition revealed a significant interaction between Time and Condition for valid trials presented in the first half of the experiment [$F(1, 12) = 7.73$, $p = .017$, $\eta_p^2 = .39$] and follow-up paired samples t-tests confirmed that there was a significant decrease in alpha amplitude from baseline to agent reappearance over left sensorimotor cortex in the A+O− condition [$t(12) = 2.60$, $p = .023$], but only a non-significant *increase* in alpha amplitude from baseline to agent reappearance in the A−O+ condition [$t(12) = 1.93$, $p = .08$]. However, while the pattern of results in the second half of the experiment was similar, the decrease in sensorimotor alpha from baseline to agent reappearance in the A+O− condition did not reach significance [$t(12) = 1.52$, $p = .16$] and again there was no decrease in activity in the A−O+ condition ($p > .9$). The fact that motor activation in response to the reappearance of
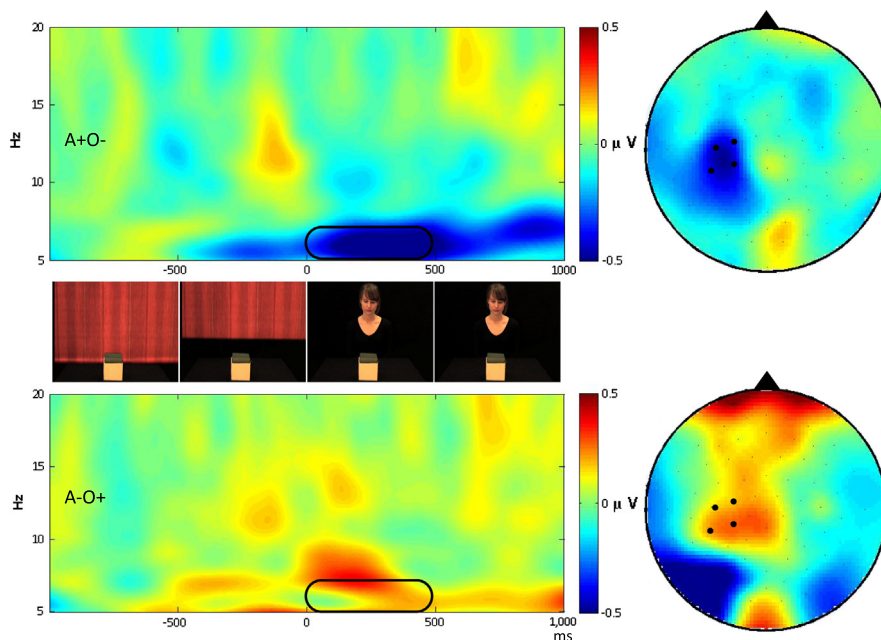

Fig. 3. Infant results. Left-hand column: Time–frequency (TF) plots for the 2 types of test trial. TF plots reflect baseline corrected activity averaged over the four left sensorimotor channels, and over all infants. Zero is the onset of the actress reappearance and activity averaged over the first 500 ms of this period was compared to the baseline period. Black rectangles indicate the time and frequency range over which statistics were computed. Right-hand column: Topographic maps showing averaged amplitude over this 500 ms analysis period and over the 5–7 Hz frequency band. Black dots indicate the 4 left sensorimotor channels over which data were averaged for statistical analysis.

the actress with a false belief that the ball is in the box (A+O−) is strongest in the first few trials strongly suggests that it is not a result of a learned association formed during the course of the experiment. Furthermore, while it is possible that associations could already be formed after only a couple of exposures, the presence of our familiarization trials provide further evidence against an association-based interpretation of our results. The four familiarization trials provided infants with evidence that, when the ball jumps into the box, the agent subsequently reaches for the box (x2), but when the ball jumps out of the box, the agent does not reach for the box (x2). Thus, if infants were indeed basing their expectations on learned associations, we should expect that their performance on those first few test trials would show the opposite pattern i.e. they would wrongly predict an action following the ball jumping into the box, but not when the ball has jumped out of the box. However, what we actually find on those first few test trials following familiarization is the opposite: an expectation of action following the ball jumping out of the box, and an expectation of no action following the ball jumping into the box.

4. Discussion

Recent work has demonstrated that young infants have an early developing propensity to track events from others' perspectives. In the current study, we go beyond these findings by showing that, not only do young infants track events from others' perspectives, but also use these representations to generate on-line action predictions. Exploiting the documented correlation between motor activation and action prediction (Caetano et al., 2007; Kilner et al., 2004; Southgate and Begus,2013; Southgate et al., 2009, 2010), we show that 6-month-old infants (and adults) make an action prediction only when it is congruent with an agent's representation of the world.

The ability to generate predictions about others' actions is crucial to successful social interactions throughout life (Blakemore & Decety, 2001; Verfaillie & Daems, 2002). For humans especially, action prediction likely plays an important role in facilitating cooperation and collaboration (Sebanz & Knoblich, 2009). Studies suggest that, by around 12 months of age, human infants are already motivated to help others attain their goals and to engage in collaborative activities with others (Knudsen & Liszkowski, 2011; Warneken & Tomasello, 2006) and an early emerging ability to predict what people will do by considering their goals and beliefs may ensure that infants are ready to take part in, and benefit from, the uniquely collaborative structure of human culture. Indeed, recent research suggests that even at 2 months, infants are already anticipating the actions of others directed towards them (Reddy, Markova, & Wallot, 2013), possibly to facilitate the smooth coordination of the action and demonstrating active participation in joint action shortly after birth.

While previous studies have used looking-time to expose young infants' sensitivity to others' beliefs, it was not clear whether infant's looking-time responses reflected a prediction concerning how an agent's representation of

events would influence her behavior. There have been a number of recent attempts to deconstruct what it is that infants are doing when they exhibit sensitivity to others' beliefs and various authors have pointed out ways in which infant's sensitivity to others' beliefs could fall short of a true understanding of belief (Apperly & Butterfill, 2011; Rakoczy, 2012). While there are many proposed requirements for a genuine understanding of belief (see Rakoczy, 2012 for a discussion of some of those), one of these requirements is that one can integrate the attributed belief with other mental states (e.g. goals) and understand the functional implications of beliefs for action (Dennett, 1989). To date, we know little about infant's appreciation of the implications of beliefs for action. For example, in the study by Kovacs et al. (2010), infants longer looking towards an outcome that should be surprising to the agent (but not to the infant) demonstrates that infants have encoded and created a representation of the event from the agent's perspective, and that this representation interferes with the representation that the infant should have of the event from their own perspective. However, it does not tell us whether infants understand anything about the functional consequences of holding a specific representation. In the current study, however, the fact that infants generate action predictions which are accurate based on consideration of the agent's representation of an event, suggests that they appreciated something of their functional consequences and thus that infants understanding of others' mental states goes beyond a mere sensitivity to belief situations (Rakoczy, 2012).

However, while the ability to predict others' object-directed actions may build upon a likely preceding ability to predict actions directed towards the infant (Reddy et al., 2013), it is unclear how infants could come to understand that others' actions should be predicted based on their beliefs. While several authors have advocated an innate, modular mechanism for attributing mental states (Carruthers, 2013; Leslie, Friedman, & German, 2004), it is also possible that infants could learn that others' actions are predictable based on certain observable factors. The early propensity to try to predict others' actions demonstrated by Reddy et al. (2013) may make infants highly sensitive to the factors that modulate others' actions, such as the physical relationship between the agent and an object (e.g. infants may begin to notice that people's heads and eyes tend to be directed towards objects that they reach for). While data gathered at 6 months cannot decide between innately-specified mechanisms exploiting mental state concepts (e.g. she will search in the box because she thinks/believes the ball to be there) or acquired contingencies (e.g. she will search in the box because she saw the object jump in), it is worth noting that what we demonstrate in this paper and describe as 'belief-based action prediction' does not necessarily imply that infants operate with a concept of belief as it is traditionally characterized (Rakoczy, 2012). In functional terms, infants are correctly predicting actions based on the other's belief state. They expect the agent to reach for the ball because the agent represents the ball as being in the box. In mental state language, they expect the agent to reach for the ball because she thinks or believes the ball to be in the box. However,

that infants are accurately predicting the agent's actions does not necessarily imply that they need be aware that what the other holds is a belief, or have any beliefs about what a belief is (e.g. that it can be true of false). While we have evidence that infants consider the perceptions of the other in generating a prediction about what the other will do, we do not know whether infants maintain this representation as an alternative representation of reality (Kovacs et al., 2010) or whether they realize that the prediction that they generate is based on a representation of the world that may or may not mirror reality (Onishi & Baillargeon, 2005; Scott & Baillargeon, 2009). Accurate predictions can be generated by considering only the others' perceptual experiences without thinking about whether the resulting representation held by the other is a true reflection of the world (Southgate, 2013). Thus one possibility might be that infants attend to those factors that are most consequential for others' actions (e.g. the object as it is represented by the other) but do not yet represent these in any relationship with the true state of affairs. In this sense, infants might represent the object as the other represents it, but they may not yet represent this representation as a belief that could be false. While this would be highly effective for predicting others' actions, it would have limited value as an explanatory mechanism (Southgate, 2013). This distinction between being capable of performing the computations necessary for generating action predictions that are consistent with the others' belief and being aware that what the other holds is a belief, maps onto the distinction between personal and sub-personal level descriptions made by Dennett. Specifically, while the data suggest that infants represent an event from the others' perspective (a sub-personal level claim), it is not clear that they understand that what results from the others' perspective is a particular mental state with particular properties (Rakoczy, 2012).

Finally, although we use motor activation as a measure of infants' ability to make belief-based action predictions, this does not imply that the motor system plays a role in *inferring* these beliefs (Gallese & Goldman, 1998). Others have made convincing arguments as to why the motor (or mirror) system is not a good candidate for mental state attributions (Jacob & Jeannerod, 2005), but our data also suggest that the motor system is unlikely to be involved in the process of attributing mental states. Mental state attributions are required to generate an accurate prediction in both the A+O− condition and the A−O+ condition. Thus, if motor representations are involved in generating inferences about the mental states that cause behavior (Gallese & Goldman, 1998), they should be recruited in both conditions. The fact that sensorimotor cortex is only recruited when the agent's false belief should cause her to reach suggests that the involvement of the motor system is one of predicting *how* the expected action will unfold (Csibra, 2007; Jacob, 2009; Southgate et al., 2010).

While previous research has demonstrated that susceptibility to others' mental states may interfere with infants' own representations of events (Kovacs et al., 2010), our data suggest that sensitivity to others' mental states also allows infants to predict what others will do next. This ability to integrate 'beliefs' with expected actions goes be-

yond what has previously been demonstrated, and suggests that young infants understanding of other minds goes beyond a mere sensitivity. Whether or not infants action predictions are mediated by a genuine concept of belief, or whether they are the product of representing the world from the others' perspective, our data demonstrate that 6-month-old infants are skilled in attending to those factors that are consequential for others' actions.

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