



PAPER

From outcome prediction to action selection: developmental change in the role of action–effect bindings

Stephan A. Verschoor,¹ Michiel Spapé,² Szilvia Biro^{1,3} and Bernhard Hommel¹

1. Leiden University Institute for Psychological Research & Leiden Institute for Brain and Cognition, The Netherlands

2. Helsinki Institute for Information Technology, Finland

3. Center for Child and Family Studies, Leiden University, The Netherlands

Abstract

Ideomotor theory considers bidirectional action–effect associations to be the fundamental building blocks for intentional action. The present study employed a novel pupillometric and oculomotor paradigm to study developmental changes in the role of action-effects in the acquisition of voluntary action. Our findings suggest that both 7- and 12-month-olds (and adults) can use acquired action–effect bindings to predict action outcomes but only 12-month-olds (and adults) showed evidence for employing action-effects to select actions. This dissociation supports the idea that infants acquire action–effect knowledge before they have developed the cognitive machinery necessary to make use of that knowledge to perform intentional actions.

Introduction

Some authors have suggested a rudimentary ability to represent action goals to be present at birth (e.g. Meltzoff & Moore, 1997; Rizzolatti & Craighero, 2004; Rochat, 2001). But where do such representations come from? Given the world's complexity and the dramatic changes the mind and body of infants undergo during development, it is rather unlikely that they are innate and permanent (Greenwald, 1970; Harless, 1861; Hommel & Elsner, 2009; James, 1890; Lotze, 1852). Piaget (1936), in his influential constructivist approach to cognitive development, firstly suggested that goals should be adaptive to the infant's changing skills and abilities and may derive from its own sensorimotor exploration and experience motivated by a predisposition to adjust to its environment. Although he states that such exploratory actions are integrated with their effects into schemata necessary for perception and action, he does not elaborate on the underlying cognitive mechanism (Piaget, 1954).

Exactly such a mechanism was proposed in the late nineteenth century, though largely neglected in psychol-

ogy for a century. Following the lead of Lotze (1852) and Harless (1861), James (1890) suggested a cognitive mechanism that does what Piaget (1936, [1963]) proposed; it provides actors with action goals that are rooted in their own sensorimotor experience. In his ideomotor theory James stated that all actions are necessarily involuntary when being carried out for the first time. Indeed, if one defines action as goal-directed movement, it presupposes some sort of anticipation of its effect. This again implies knowledge on action–effect relationships, which needs to be acquired before the action can be carried out 'in order to' produce the outcome intentionally. Ideomotor theory suggests that such knowledge is acquired on the fly: whenever people move, they automatically and unintentionally create bidirectional associations between the perceived effects and the motor pattern producing them. This association brings the movement under voluntary control: Once acquired, the agent can now activate the motor pattern producing a movement by 'thinking of' (i.e. endogenously activating the representation of) a perceptual effect. Indeed, infants start to motor babble (i.e. produce random movements) *in utero* (cf. Meltzoff & Moore,

1997) – which could explain the possible presence of goal representations at birth – and they are consistently exploring their environment. This provides ample opportunity to acquire movement/action–effect associations and thus a steadily increasing pool of possible action goals. Thus, James considered bidirectional movement/action–effect associations the fundamental building blocks of intentional action and provides a mechanism that could allow the emergence of goal-directed action in infants.

Ideomotor theory was revived and refined by Greenwald (1970), Prinz (1990, 1997), and Hommel (1996; Elsner & Hommel, 2001) and is now part of a broader theoretical movement stressing the interplay between perception and action (Hommel, Müsseler, Aschersleben & Prinz, 2001; Meltzoff, 2006; Meltzoff & Prinz, 2002). This motivated numerous demonstrations of bidirectional action–effect acquisition in humans ranging from 4-year-olds (Eenshuistra, Weidema & Hommel, 2004; Kray, Eenshuistra, Kerstner, Weidema & Hommel, 2006) to adults (Elsner & Hommel, 2001). Action–effect acquisition was found for a wide range of actions and effects (for a review see Hommel & Elsner, 2009), suggesting a general action–effect integration mechanism. In addition, action–effect acquisition has been found after just one trial (Dutzi & Hommel, 2009), suggesting that the mechanism is fast-acting and implicit. Action–effect acquisition is modulated by the same factors that influence instrumental learning (e.g. temporal contiguity and contingency of movement and effect; Elsner & Hommel, 2004) and does not depend on voluntary attention (Dutzi & Hommel, 2009; Elsner & Hommel, 2001; Band, van Steenbergen, Ridderinkhof, Falkenstein & Hommel, 2009). Together with the fact that it was also found in animals (see Elsner & Hommel, 2001), this suggests that action–effect integration is a fairly low-level and automatic process (Elsner & Hommel, 2004).

If bidirectional action–effect associations are indeed the fundamental building blocks for intentional action, the system that generates these associations should be operative early in life. Especially since infants show evidence of goal-directed behavior from a very early age on: depending on the definition, goal-directed behavior is thought to start somewhere between birth (Meltzoff & Moore, 1997; von Hofsten, 2004) and about 9 months of age (Hauf, 2007; Piaget, 1936, [1963]). Action–effect knowledge has been implicated to be operational in higher order cognitive functions such as action understanding in 7-month-olds (e.g. Biro & Leslie, 2007; for a review, see Hauf, 2007; Schneider, Eschman & Zuccolotto, 2002) and imitation in 9-month-olds (Hauf & Aschersleben, 2008; Klein, Hauf & Aschersleben, 2006;

for a review, see Elsner, 2007; Meltzoff, 2006). Even though these findings do not provide direct evidence for bidirectional action–effect acquisition, theories that emphasize similar representational formats for first-person experience and observed action (e.g. Fabbri-Destro & Rizzolatti, 2008; Hommel *et al.*, 2001; Meltzoff, 2006; Tomasello, 1999), and conceptualize action understanding as inverse planning (Meltzoff, 2006; Baker, Saxe & Tenenbaum, 2009) consider them corroborative. Other corroborating evidence was found in studies that show very young infants to be sensitive to action–effect contingencies. For instance, newborns actively adjust their sucking rate in response to their mother's voice as ongoing conditional feedback (DeCasper & Fifer, 1980) and 2-month-olds pursue interesting action effects by intentionally varying their sucking rate (Rochat & Striano, 1999) or varying gaze direction (Watson, 1967; for a review, see Gergely & Watson, 1999). Another line of research by Carolyn Rovee-Collier shows that action effects aid memory retrieval for actions from 2 months of age (Rovee & Rovee, 1969; for a review, see Rovee-Collier, 1999). Telling as these studies may be (they show that action contingent effects play an important role in infant behavior and memory), they were not designed to directly assess the bidirectionality of action–effect associations and their use for action planning and may thus confound actual action–effect learning with simple operant conditioning. Nonetheless, these findings may reflect a developing ability for learning action–effect contingencies.

The first study to find direct evidence for bidirectional action–effect associations in infants was undertaken by Verschoor, Weidema, Biro & Hommel (2010) with 9-, 12- and 18-month-old participants. A simplified version of the free-choice design of Elsner and Hommel (2001) was used. In the acquisition there were two types of trial: One in which infants were permitted to touch a response key, which resulted in a particular audiovisual effect, and another in which they were prevented from touching the key while another audiovisual effect was presented. When the two effects were replayed in the test phase, all infants were faster to touch the key again after the previously self-produced effect than after the action-independent effect. Moreover, the 18-month-olds responded more often following the self-produced effect. These results were taken as evidence for bidirectional action–effect learning, since the self-produced effect activated the response that previously caused the effect. Although this study shows direct evidence for action–effect learning in infants, the paradigm had some drawbacks compared to the Elsner and Hommel (2001) paradigm. The paradigm had only 10 acquisition trials and two test trials which resulted in slightly noisy data,

and due to the nature of the task the paradigm was unsuited for comparison with adults. Thus it remains to be seen whether bidirectional action–effect learning works similarly in infants and adults. Furthermore, initial piloting showed that, due to difficulties with the button pushing action, it was unsuitable for infants younger than 9 months (Verschoor *et al.*, 2010).

Overcoming these limitations calls for a more natural type of action that is well established in very young infants. Eye movements seem to be the ideal candidate: infants have been reported to actively and accurately control their eye movements from at least 4 months of age (Scerif, Karmiloff-Smith, Campos, Elsabbagh, Driver & Cornish, 2005) and, given that infants actively control their gaze to gather information (Gredebäck & Melinder, 2010; Falck-Ytter, Gredebäck & von Hofsten, 2006), to direct or follow attention (Perra & Gattis, 2010), and to engage in social behaviors (Senju & Csibra, 2008; Johnson, Ok & Luo, 2007), eye movements can be considered truly goal-directed actions. Moreover, a study by Herwig and Horstmann (2011) demonstrated saccade-effect learning in adults in a paradigm conceptually very close to that of Elsner and Hommel (2001), which indicates that action–effect integration generalizes to oculomotor action.

In the present study, participants made eye movements towards visual stimuli appearing at the left or right of a display, the two directions produced different auditory effects – analogous to the Elsner and Hommel (2001) paradigm. In the subsequent test phase, participants were presented with the effect tones and could freely choose to make a saccade to the left or right of two simultaneously presented visual stimuli. We expected that the tone would prime the saccade that it was produced by in the acquisition phase, so that this saccade would be chosen more frequently and/or initiated more quickly. This design allowed us to test both infants younger than 9 months of age and adults, and to run considerably more trials.

We tested 7- and 12-month-olds and adults. Seven-month-olds were chosen because this group is known to show understanding of goal-directed actions (e.g. Woodward, 1998; Csibra, 2008; Verschoor & Biro, 2012). Since some action–perception theorists (Hommel *et al.*, 2001; Meltzoff, 2006; Meltzoff & Prinz, 2002; Woodward, 2009; Rizolatti & Craighero, 2004) stress that the same representational format is used for observed and self-initiated action, even 7-month-olds should be able to pick up action–effect associations. A first study that shows action–effect acquisition in infants younger than 9 months was recently published by Paulus, Hinnius, Elk and Beckering (2012). They found electrophysiological evidence indicating that

infants at 8 months of age show stronger motor resonance when listening to previously self-produced action-related sounds than when hearing other sounds. It remains to be seen whether the underlying action–effect associations are bidirectional in the sense that they can be reversed to generate overt action. Dissociations between acquired action knowledge and the use of such knowledge are by no means new; for instance Keen (2005) found a similar dissociation in her work on reaching and looking for occluded objects which shows that infants' looking behavior exhibits knowledge while actions do not conform to this knowledge. In a more general sense, such dissociations are apparent in looking-time studies wherein infants are reported to possess knowledge on actions they cannot perform themselves (e.g. Verschoor & Biro, 2012; Csibra, Gergely, Biro & Koós, 1999).

To maximize the chance of finding developmental changes in this study, we included the older of the two youngest groups in Verschoor *et al.* (2010) since no differences were found between 9- and 12-month-olds in that study. They were also included to replicate Verschoor *et al.*'s (2010) finding that infants at this age show bidirectional action–effect learning and to contrast this ability with the suggested inability of the 7-month-olds to initiate true intentional action (Hauf, 2007). We included adults to confirm that the same principles of bidirectional action–effect learning can be shown in 12-month-old infants and adults.

Using an eye-tracker enabled us to measure not only the choice of actions and the time to initiate them (reaction time), but pupil size as well. This is a relatively new measure in developmental studies (e.g. Falck-Ytter, 2008; Jackson & Sirois, 2009; Gredebäck & Melinder, 2010; for a review, see Laeng, Sirois & Gredebäck, 2012) but has been extensively used in psychological research on adults since the early 20th century (Hess, 1975). Pupils have the interesting characteristic of reacting not only to luminance, they reliably dilate with superimposed sympathetic activation (Libby, Lacey & Lacey, 1973; Beatty & Lucero-Wagoner, 2000). Although these dilations are not directly causally related to central processing load, they empirically reflect variations in central processing load with extraordinary precision (Beatty & Lucero-Wagoner, 2000). Task-Evoked Pupillary Responses (TEPRs) can indicate motivational phenomena such as arousal (Bradley, Miccoli, Escrig & Lang, 2008; Laeng & Falkenberg, 2007), attention allocation (e.g. Hess & Polt, 1960), cognitive load (Kahneman & Beatty, 1966), and mental effort (Kahneman, 1973; Hess & Polt, 1964). TEPRs are pre-conscious and mediated by the locus coeruleus (Laeng *et al.*, 2012). Whatever the exact interpretation of this measure, using it enables us

to contrast acquisition contingent vs. non-contingent responses: whether TEPRs are taken to reflect differences in sympathetic activation in general or arousal, attention allocation, cognitive load or mental effort, all interpretations suggest that dilations should be larger for incongruent responses.

We assumed that in our task two types of process might play a role and affect TEPRs. For one, even in studies that were successful in demonstrating that action effects bias the choice of actions (e.g. Elsner & Hommel, 2001), participants did not always choose the action that was previously associated with the present trigger stimulus. To some degree, this might be due to random noise but it may also reflect a strategy to create some variability and exert active control. Exerting control calls for the investment of more cognitive resources, which would suggest that selecting and/or performing an action that is not associated with, and thus primed by, the trigger stimulus is more effortful. If so, one would expect that choices of tone-incongruent actions (i.e. of an action different from the one that previously produced the present trigger stimulus) are accompanied by (greater) pupil dilation.

For another, there is evidence that action–effect associations not only affect the choice of actions but also their evaluation. In the study of Band *et al.* (2009), participants performed a probabilistic learning task, in which key-presses triggered tones of a particular pitch in 80% of the trials and of another pitch in the remaining trials. The presentation of a less frequent action effect generated an electrophysiological component that is known as feedback-related negativity (Miltner, Braun & Coles, 1997), which is commonly observed when negative feedback is presented. This suggests that action–effect associations are used to generate particular expectations about effects given the execution of a particular action. In infant studies, TEPRs have been used as an index of the violation of expectations (Jackson & Sirois, 2009; Gredebäck & Melinder, 2010). Accordingly, it is possible that carrying out a tone-incongruent action results in (more) pupil dilation reflecting the violation of a tone-induced expectation regarding the action outcome (i.e. the location of the action end point and/or the targeted stimulus).

Although both processes would predict greater pupil dilations in incongruent responses, we considered that these might be distinguished in terms of their temporal dynamics: whereas a choice-related process would be likely to affect pupil responses briefly before or after response execution, an expectation/evaluation-related process would be more likely to affect pupil responses after response execution (Band *et al.*, 2009).

Methods

Subjects

Two groups of infants were tested: 15 7-month-olds (mean: 7.15 months, $SD = .21$, $SE = .05$, 8 female) and 20 12-month-olds (mean: 12.11 months, $SD = .26$, $SE = .05$, 9 female). The infants were recruited through direct mail. Informed consent and answers to a questionnaire regarding their general health were obtained from all caretakers. The infants were all healthy full-term and without any pre- or perinatal complications. In addition, 24 undergraduate students (mean age: 23.8 years, $SD = 2.47$, $SE = .50$, 14 female) participated in exchange for course credits. All reported being healthy and having normal or corrected-to-normal vision and hearing. Two additional 12-month-olds and one adult were excluded due to technical error, and two more 7- and four 12-month-olds were excluded due to fussiness. In addition, two 7- and two 12-month-olds were excluded for not meeting the criterion for the minimal amount of test trials.

Test environment and apparatus

During the experiment participants sat in a specially designed stimulus-poor curtained booth (infants on the lap of their caretaker) in front of the monitor/eye-tracker apparatus. The distance between eyes and apparatus was approximately 70 cm (the screen's viewing angle was 34.1° by 21.8°). Participant behavior was monitored online by means of a camera located above the apparatus. The experimenter controlled the experiment from a separate control room. A 17-inch TFT screen, equipped with an integrated Tobii T120 eye-tracker operating at 60 Hz, was used for visual and auditory data presentation, and for data collection. The Tobii T120 has an average accuracy of .5 visual degrees and allows for a reasonable amount of free head movement by the subject (30 × 22 × 30 cm). It recorded gaze direction and pupil size. Stimulus presentation was controlled by a PC running E-prime[®] software (Schneider, Eschman & Zuccolotto, 2002).

Procedure

Infants were tested at a time of day when they were likely to be alert and in a good mood. Caretakers and participants were given instructions prior to the experiment. Adults were given no instruction with regard to the task. The caretakers were instructed not to move after calibration and gently fixate the infant against their

tummy to maintain the eye-tracker alignment and to entertain the infant during the 1-min interruption between calibration and the experiment. The eye-tracker was calibrated using a 9-point calibration consisting of an animated dancing infant accompanied by music. The calibration was accepted with a minimum of eight points acquired successfully. The experimenter could play an attention-grabbing sound during the experiment to regain attention. If the attention grabbing sound did not work, caretakers were encouraged to direct the infant's attention to the middle of the screen by pointing to it. Lighting conditions were kept constant during testing and across subjects. Furthermore, the luminance levels were controlled for by presenting the stimuli in a random fashion. After completion of the experiment, further information on the rationale was provided.

Acquisition Phase

The experiment began with an acquisition-phase of 48 trials (see Figure 1). The background color of the screen was gray. An acquisition trial started with a brightly colored dot with a superimposed line drawing (4.3° by 4.3°) being displayed at the center of the screen (Snodgrass & Vanderwart, 1980). The dot served as start signal and fixation mark. To keep the display interesting to the subjects, the color of the dot changed randomly from trial to trial (selected from eight bright colors) and the superimposed line drawing was randomly selected (without replacement) from a selection of 50 drawings. The dot disappeared after the subject fixated properly for an interval that varied from trial to trial (so to remove any

bias or habituation that might be caused by fixed intervals between trials) between 150 and 350 ms.

Immediately after the dot disappeared, photographs of two different faces (randomly selected without replacement from 100 grayscale pictures from the 'Nottingham scans' emotional faces database, <http://pics.psych.stir.ac.uk>, displaying emotionally neutral faces of 50 men and 50 women from a frontal perspective) appeared left and right from the dot. Faces were chosen to elicit spontaneous saccades as they are known to attract infants' attention (Goren, Sarty & Wu, 1975; Johnson, Dziurawiec, Ellis & Morton, 1991). The 5.3° by 5.3° pictures appeared at 9.7° , center to center, to the left and right of the center of the screen. To avoid perseverance to either left or right across acquisition trials, the images immediately started to pulsate. One of the faces started shrinking to 4.1° while the other started growing to 6.5° (which picture started shrinking was randomized); one cycle from intermediate size to small, to intermediate, to large and back to intermediate, took 2 s.

The faces evoked spontaneous saccades and thus served as response locations. When a saccade towards one of the two face locations was detected, the face at the other location disappeared. The targeted face stopped pulsating and, depending on the targeted side, one of two distinct 200-ms effect sounds ('tring' or 'piew') was presented. Each effect-sound was consistently designated to either the left or the right response area (RA) during the entire acquisition phase (the mapping was balanced across participants); RAs were defined as the maximum size of the pulsating images: 6.5° by 6.5° . A saccadic response was defined as an eye movement to the left or

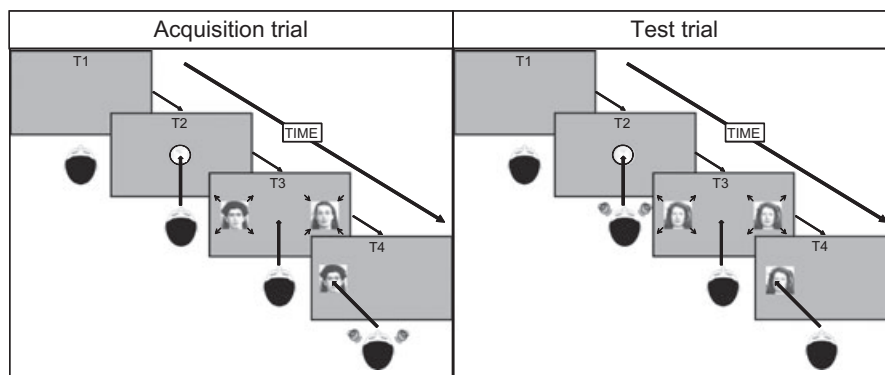


Figure 1 *Acquisition trial* T1: Each trial starts with an intertrial interval of 500 ms. T2: A fixation dot is displayed at screen center. T3: After successful fixation, faces appear at either side of the screen where they started to pulsate. T4: Depending on the saccade target, the face at the other side disappears and an effect sound is played for 200 ms. *Test trial* T1: Each trial starts with an intertrial interval of 500 ms. T2: A fixation dot is displayed at screen center. After successful fixation one of the previous action effects is played. T3: The dot disappears and thereafter the same face appears on both sides. T4: The participant freely chooses where to saccade.

right response area (minimal amplitude 4.3°). Reaction Times (RTs) were defined as the time it took from the disappearance of the central dot to the time one of the RAs was entered. The maximum allowable RT was defined as 2000 ms; when subjects did not respond within this time the same trial was repeated. After each trial, an inter-trial interval of 500 ms was presented. If during the acquisition phase the subject showed declining attention to the screen or was otherwise distracted, the acquisition phase could be shortened (minimum amount of acquisition trials was set at 30).

Test phase

After acquisition, the test phase followed directly (32 trials) (see Figure 1). A test trial started with a similar dot with superimposed line drawing as in the acquisition phase, again serving as a start and fixation stimulus. However, after the subjects fixated on the dot (fixation time again varied randomly between 150 and 350 ms), the dot stayed on the screen for another 200 ms during which one of the effect sounds that was previously triggered by one of the two eye movements, was played after which the dot immediately disappeared. Then two identical 5.3° by 5.3° images of the same face (again randomly selected without replacement from the Nottingham scans emotional faces database) appeared 9.7° to the left and right of the center of the screen. The images were identical to avoid any influence on the subject's gaze preference. To further minimize influence on preference, the faces now pulsed in synchrony; they both either started growing or shrinking (randomized and with the same motion parameters as in the acquisition). Again, this was expected to evoke a spontaneous saccade and the question of interest was whether the direction of this saccade would be biased by the tone. Saccades towards the location that previously produced the tone were considered congruent, while saccades towards the alternative location were considered incongruent. The minimum number of test trials to enter analysis was 21. Except for the absence of the effect after the saccade, the remaining procedure was as in the acquisition phase.

Awareness

After the experiment, adults were asked if they noticed any regularity in the sound mapping in the experiment. If so, they were asked what it was (e.g. 'When I looked to the right I heard sound X, when looking to left I heard sound Y'). Then, all subjects were asked whether they noticed that there were two parts to the experiment. If

they did notice, they were asked more specifically if they noticed any regularity in the sounds during the first (acquisition) phase; if not, they were scored as unaware. If they noticed two phases but no regularity in the sound mapping, they were asked specifically if they had noticed that during the first phase there was a mapping between sounds and direction of looking. If they did they were considered 'aware', otherwise 'unaware'.

Data acquisition

E-prime[®] was used to collect RTs during acquisition and test phases, the number of left and right responses during acquisition, and the number of congruent and incongruent responses during test. Furthermore, the E-gaze data files produced by E-prime[®] were imported into BrainVision Analyzer software (Version 1.05, BrainProducts, Germany) to analyze gaze position and pupillary data. First, pupil sizes of both eyes were averaged to create more stable data. Artifacts and blinks as detected by the eye-tracker were corrected by using a linear interpolation algorithm. After this a 10 Hz low-pass filter was used, commonly used for pupil data (e.g. Hupe, Lamirel & Lorenceau, 2009). To ensure that there were no erroneous pupil data we then rejected artifacts using the parameters of a minimal pupil size of 1 mm and a maximum of 5 mm; furthermore, the maximum allowed change in pupil size was defined as .03 mm in 17 ms.

Given that the acquisition of action–effect associations is sensitive to the same factors as stimulus–response learning (Elsner & Hommel, 2004), the bias to respond in either direction during acquisition was calculated ('Acquisition Bias', AB = the number of leftward saccades minus the number of rightward saccades). As the size of this bias represents the degree to which participants were selectively exposed to one of the action effects, the AB variable was used as covariate in the analyses when appropriate.

Results

Acquisition phase

RT and response frequency

All ANOVAs were performed with age group as a between-subjects factor. ANOVAs on the percentage of left responses and number of completed acquisition trials showed no effects, $ps > .3$ (see Table 1).

Another ANOVA, on mean RT, revealed a significant effect of age group, $F(2, 56) = 55.30$, $p < .001$,

Table 1 Mean scores of acquisition phase (standard deviation in parentheses)

Age group scores	Number of acquisition trials	Percentage of left responses	RT in ms
7-month-olds	47.1 (3.36)	60.3 (37)	441 (49)
12-month-olds	47.15 (2.30)	48.9 (30)	440 (57)
Adults	48 (0)	52.4 (11)	293 (50)

$\eta^2p = .66$: post-hoc Tukey HSD comparisons revealed that adults responded significantly faster than infants, $ps < .001$, (see Table 1).

A repeated-measures ANOVA on RTs with right-vs.-left as within-subjects factor showed no effects, $ps > .8$.

Awareness

Only four out of 24 adult participants reported being aware of the action–effect mapping in the acquisition phase.

Test phase

Response frequency

Again all ANOVAs were performed with age group as a between-subjects factor. An ANOVA on the number of completed test trials showed a significant effect of age group, $F(2, 56) = 7.71$, $p = .001$, $\eta^2p = .22$. Post-hoc Tukey HSD comparisons revealed that adults and 7-month-olds completed more test trials than 12-month-olds (mean adults = 32, 7-month-olds = 31.6, 12-month-olds = 29.6, $ps < .02$). This is probably due to increased agility and fussiness in the 12-month-olds and increased motivation in the adults (see Table 2).

A repeated-measures ANOVA on percentage of responses with left vs. right as within-subjects factor revealed that, overall, participants showed no tendency to saccade more often to either side, $p > .05$; however, it did show an interaction with age group, $F(2, 52) = 4.11$, $p = .02$, $\eta^2p = .14$. Separate comparison showed that while adults made more leftward saccades, $F(1, 23) = 4.23$, $p = .05$, $\eta^2p = .16$ (18 left vs. 14 right), 12-

month-olds did the opposite, $F(1, 18) = 5.94$, $p = .03$, $\eta^2p = .25$ (12 left vs. 18 right) (see Table 2).

More importantly for our purposes, a repeated-measures ANOVA on response frequency with congruency as within-subjects factor showed that the percentage of acquisition-congruent vs. incongruent responses did not differ and congruency did not interact with age group, $ps > .6$.

In addition, we performed a median split on RTs on each subject, classifying trials as either fast or slow, and calculated the percentage of fast congruent responses vs. the percentage of slow congruent responses. We then performed a repeated-measures ANOVA on the percentage of congruent responses, with fast vs. slow as within-subjects factor. We found no main effect of fast vs. slow on percentage ($F > 1$), but we did find a significant interaction of fast vs. slow with age group, $F(1, 56) = 3.58$, $p = .03$, $\eta^2p = .11$. We then tested the age groups separately, showing that adults had a higher percentage of congruent responses in their fast responses compared to their slow responses (54% vs. 45%), $F(1, 23) = 11.5$, $p = .003$, $\eta^2p = .33$, while the infants showed no such effect (see Table 2).

We also performed a repeated-measures ANOVA on percentage of congruent reactions with Time (dividing the responses into three bins; trial 1–10, 11–21 and 22–32) as within-subjects factor which did not yield any effects, $ps > .2$.

Reaction times

Again all ANOVAs were performed with age group as a between-subjects factor. Since the test phase was self-paced we also performed an ANOVA on inter-trial interval (ITI) and found a significant effect, $F(2, 56) = 36.53$, $p < .001$, $\eta^2p = .57$. Post-hoc Tukey HSD comparisons revealed that adults responded significantly faster than infants, $ps < .001$ (see Table 3).

As in the acquisition phase, an ANOVA on RTs showed that adults responded faster than the two infant age groups, $F(2, 56) = 89.07$, $p < .001$, $\eta^2p = .76$; all HSD $ps < .001$.

Table 2 Mean frequency scores of test phase (standard deviation in parentheses)

Age group scores	Completed test trials	Percentage of left responses	Percentage of congruent responses	Percentage of congruent responses in fast reactions	Percentage of congruent responses in slow reactions
7-month-olds	31.6 (1.55)	61.5 (34.9)	48.8 (6.9)	46.3 (12.4)	51.3 (12.6)
12-month-olds	29.6 (3.44)	38.1 (28.7)	49.8 (6.6)	51.8 (6.7)	47.6 (13.3)
Adults	32 (0)	56.5 (15.5)	49.7 (10.9)	54.4 (13.5)	45.1 (12.4)

Table 3 Mean RT scores of test phase (standard deviation in parentheses)

Age group scores in ms	ITI	RT	RT Congruent	RT Incongruent	RT trial 1–10	RT trial 11–21	RT trial 22–32
7-month-olds	2761 (842)	432 (71.9)	437.6 (77.9)	425.0 (78.0)	410.1 (71.1)	427.8 (74.7)	426.9 (109.5)
12-month-olds	2807 (902)	449 (62.3)	427.4 (60.5)	470.6 (83.4)	420.9 (85.7)	431.2 (53.8)	493.6 (104.7)
Adults	1218 (255)	237.6 (42.9)	230.4 (47.4)	244.0 (39.2)	245.9 (47.6)	234.8 (49.4)	229.2 (49.2)

Another repeated-measures ANOVA on RT's with left vs. right as within-subjects factor showed no effect, $p > .1$ (see Table 3).

More importantly for our purposes, we performed a repeated-measures ANOVA on RTs with congruent vs. incongruent as within-subjects factor, using AB as a covariate which showed that acquisition-congruent responses were initiated 14 ms faster than incongruent responses, $F(1, 55) = 4.20$, $p = .05$, $\eta^2p = .07$, and this effect interacted with age group, $F(2, 55) = 4.38$, $p = .02$, $\eta^2p = .14$. Separate comparisons showed that the congruency effect was significant in adults, $F(1, 22) = 10.60$, $p = .004$, $\eta^2p = .33$, and 12-month-olds, $F(1, 18) = 8.51$, $p = .009$, $\eta^2p = .32$, but not in 7-month-olds, $F(1, 13) = 2.51$, $p = .14$ (see Figure 2). Additional non-parametric analysis in the 7-month-olds also failed to show an effect of congruency on RTs in this group (see Table 3).

We also performed a repeated-measures ANOVA on RTs with Time (dividing the responses in three bins; trial 1–10, 11–21 and 22–32) and congruence as within-subject factors using AB as a covariate. We found an overall tendency regarding the main factor of Time, ($F(2, 102) = 2.64$, $p = .08$, $\eta^2p = .05$) with slower responses as the test progressed which interacted with

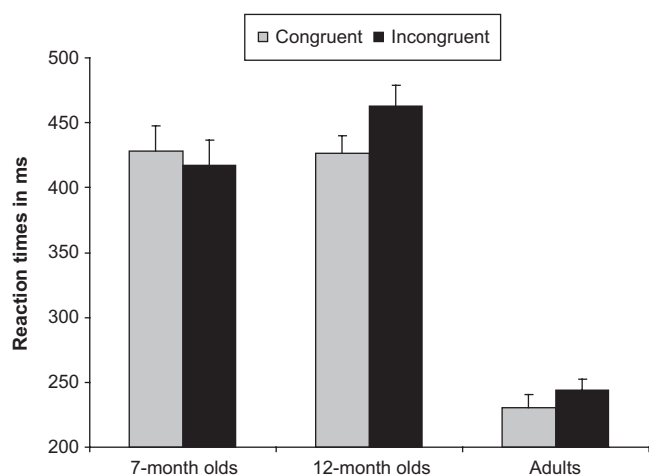


Figure 2 Mean reaction times (+SE) for adults ($N = 24$) 7-month-olds ($N = 17$) and 12-month-olds ($N = 22$) in congruent and incongruent test trials.

age group, $F(4, 102) = 3.72$, $p = .01$, $\eta^2p = .13$, and further separate testing revealed that only the 12-month-olds showed a significant slowing as the test progressed, $F(2, 32) = 7.02$, $p = .003$, $\eta^2p = .31$. No further interactions with Time were found, $ps > .3$. The main effect of congruency on RTs was significant, $F(1, 51) = 10.85$, $p = .002$, $\eta^2p = .18$, and showed that congruent responses were initiated 23 ms faster. The interaction of congruency with age group on RTs also reached significance, $F(2, 51) = 5.70$, $p = .006$, $\eta^2p = .18$. Separate testing for the age groups revealed that the effect was significant in adults, $F(1, 21) = 7.45$, $p = .013$, $\eta^2p = .26$, and in the 12-month-olds, $F(1, 16) = 13.90$, $p = .002$, $\eta^2p = .47$, but not in 7-month-olds, $F(1, 12) = .95$, $p = .35$ (see Table 3).

Pupil dilation

TEPRs were sorted according to congruency of the response and the stimulus- and response-locked time functions were averaged. Segments were created, depending on the analysis, from 2000 ms before the presentation of the sound or RT to 8000 ms after while allowing for overlapping segments. Following the method used by Bradley *et al.* (2008), pupil diameter measurement began after the initial pupil reflex caused by the fixation stimulus. Visual inspection showed the light reflex to end around 500 ms after effect presentation (see Figure 3). To accommodate for the variable RTs across age groups and conditions, we considered both stimulus-locked and response-locked TEPRs. TEPRs were calculated as the percentage of dilation relative to the baseline to make the data more comparable across age groups.

First we analyzed whether the percentage of trials rejected due to erroneous data points differed across age groups. An ANOVA on the percentage of kept trials yielded a reliable main effect of age group, $F(2, 56) = 4.30$, $p = .02$, $\eta^2p = .13$ (average percentage of kept trials: 7-month-olds 92%, 12-month-olds 92%, adults 99%). Post-hoc Tukey HSD comparisons showed that in adults significantly fewer segments were rejected than in the 12-month-olds, $p = .03$, and the same tendency was visible in the comparison of adults and 7-month-olds,

$p = .08$, an unsurprising observation given the differences in attentional resources between infants and adults.

The stimulus-locked analysis of TEPRs in congruent and incongruent trials used a 500 ms pre-effect baseline (Beatty & Lucero-Wagoner, 2000). A repeated-measures ANOVA on pupil dilations with congruency as within-subjects factor revealed no a priori effects of congruence on baselines (-500 to 0 ms), $ps > .10$. TEPRs start from 200 to 300 ms after stimulus onset and peak around 1200 ms post-stimulus (Beatty & Lucero-Wagoner, 2000) in the range of 500 ms to 2000 ms (Beatty, 1982). We therefore calculated the mean TEPRs for congruent and incongruent responses as the mean percentage of change from baseline to 500–2000 ms post effect onset.

A repeated-measures ANOVA revealed that, overall, participants showed larger relative dilations in incongruent trials, $F(1, 56) = 6.80$, $p = .01$, $\eta^2p = .11$, and this effect was not modulated by age group, $p > .10$ (see Figure 3). To take a closer look into developmental changes, we then analyzed the infant data separately. On average, infants showed larger relative dilations in incongruent trials, $F(1, 33) = 6.78$, $p = .02$, $\eta^2p = .17$, and this effect was not modulated by age group, $p > .10$. Of particular importance (given the reaction time results), the congruency effect remained significant when the 7-month-olds were tested separately, $F(1, 14) = 12.0$, $p = .004$, $\eta^2p = .46$.

For the response-locked analysis, we calculated the percentage of dilation from a 700-ms time window from saccade onset on, to a 200-ms pre-response baseline. A repeated-measures ANOVA showed no a priori effects of congruence on baselines (-200 to 0 ms), $ps > .10$. The analysis of these data yielded a significantly larger relative dilation in incongruent than congruent trials, $F(1, 56) = 7.82$, $p = .007$, $\eta^2p = .12$, while the interaction with age group was not significant, $p > .10$ (see Figure 4). A separate analysis of the infant data showed

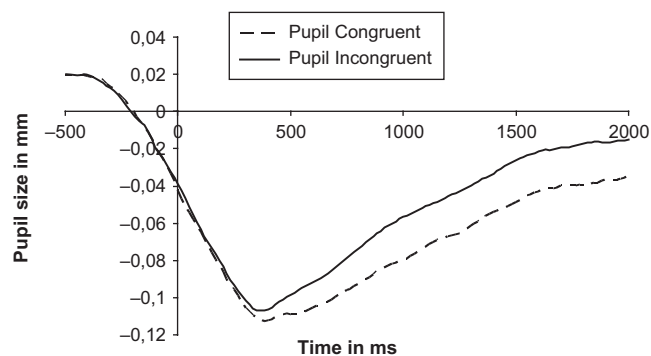


Figure 3 Mean relative pupil sizes for congruent and incongruent responses, stimulus-locked.

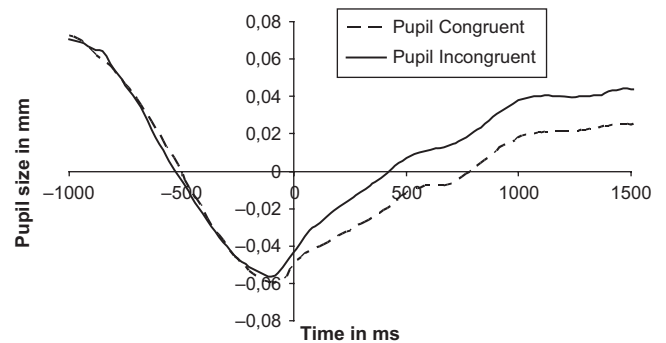


Figure 4 Mean relative pupil sizes for congruent and incongruent responses, response-locked.

a main effect for congruency, $F(1, 33) = 8.41$, $p = .007$, $\eta^2p = .20$, that was not modulated by age group, $p > .10$.

Another version of this analysis with a 1000-ms pre-response baseline produced a different pattern (a repeated-measures ANOVA revealed no a priori effects of congruence on baselines, $ps > .10$): a congruency effect, $F(1, 56) = 10.19$, $p = .001$, $\eta^2p = .17$ (see Figure 4), but also an interaction of congruency with age group, $F(2, 56) = 3.99$, $p = .02$, $\eta^2p = .13$. Separate testing showed that the effect was only reliable in the 7-month-olds, $F(1, 14) = 10.59$, $p = .006$, $\eta^2p = .43$, while the other two groups did not reach significance.

Discussion

The aim of the current study was to directly compare action–effect learning in infants and adults using a novel paradigm that relies on oculomotor actions that occur spontaneously and do not require verbal instruction. We succeeded in developing an eye-tracking paradigm that was equally suitable for both very young infants and adults. Moreover, the paradigm allowed for concurrently investigating the impact of action–effect learning on biases in, and the efficiency of, action selection as measured by response choice and RT, respectively, and on action effort and/or monitoring, as indicated by pupil dilation.

As expected from ideomotor theory (James, 1890; Hommel *et al.*, 2001), adults and 12-month-olds were faster in carrying out responses that were congruent with the present trigger tone (i.e. responses that produced this tone in the acquisition phase) than incongruent responses. The only difference between congruent and incongruent responses was their past relationship with the tones, which indicates that the congruency effect reflects associative knowledge acquired during the

acquisition phase. Moreover, the fact that the tones now primed the response they previously had followed suggests that the underlying association was bidirectional in nature. Both observations are consistent with ideomotor theory and fit well with the observations of Herwig and Horstmann (2010), who reported oculomotor action–effect learning in adults. Interestingly, these authors used visual action effects while the present study employed auditory effects. This confirms that the mechanism underlying action–effect learning is general and is not bound to a particular modality, as long as the effects are contingent on, and temporally close to, the corresponding actions (Elsner & Hommel, 2004). We also found that most adults were unaware of the saccade–effect mapping, which is in line with the idea that action–effect acquisition is a low-level, fast and automatic process that does not require attention. It seems reasonable to assume that the same holds for the infants.

The present findings fit with observations from manual actions in a developmental study of action–effect acquisition by Verschoor *et al.* (2010). In this study, reliable RT effects were found in 9-, 12- and 18-month-olds, indicating action–effect acquisition in these age groups. We obtained a similar RT effect in 12- but not 7-month-olds. We take this to imply that, although ongoing contingent action–effects can influence behavior and memory at this age (Gergely & Watson, 1999; Rovee-Collier, 1999), action–effect associations cannot yet be reversed to play an active role in prospective action control. This is in line with the dissociation between acquired action knowledge and the use of such knowledge found by Keen (2005) and Sommerville, Woodward and Needham (2005). It also fits with similar dissociations in looking-time studies wherein infants are reported to possess knowledge of actions they cannot perform themselves (e.g. Verschoor & Biro, 2012; Csibra *et al.*, 1999).

Although we found an effect in the adults indicating that fast responses were more likely to be acquisition-congruent than slow responses (this can be taken as further evidence that action–effect learning relies on a fast and automatic mechanism, at least in adults), congruency effects were restricted to RTs and did not affect response choice. One might assume that the lack of frequency effects suggests different developmental pathways with respect to manual and oculomotor actions. There are several arguments against this interpretation. For one, although manual free-choice studies have shown that presenting an action effect can bias response choice towards the response that had previously produced that effect in adults (e.g. Elsner & Hommel, 2001; Eenshuistra *et al.*, 2004; Kray *et al.*, 2006), even in free-choice studies that did find a reliable effect on response

frequency, frequency turned out to be less sensitive to action–effect learning than reaction time. For instance, Verschoor *et al.* (2010) obtained a congruency effect on response frequency in 18-month-olds, but not in younger infants, while congruency affected reaction time in 12- and 9-month-olds as well. Since Verschoor *et al.* (2010) used only very few test trials, one might suggest that in their study extinction, which younger infants are more susceptible to (e.g. Hartshorn, Rovee-Collier, Gerhardstein, Bhatt, Wondoloski, Klein, Gilch, Wurzel & Campos-de-Carvalho, 1997), could not have played a major role. In the present study the test phase contained considerably more test trials (which were necessary to get sufficiently clean pupil dilation data). Our paradigm thus provided more opportunity for extinction since action effects were no longer presented during test trials. However, we tested whether the effect of congruency on RT's and response frequency declined over time and found no such effect. Even though action–effect learning can be demonstrated under extinction conditions in principle, extinction does make the effect weaker (Elsner & Hommel, 2001) – and it may have weakened it enough to selectively annihilate the frequency effect altogether. Moreover, Herwig and Horstmann (2011) showed under extinction conditions a reliable reaction time effect in their very similar, albeit forced-choice oculomotor paradigm using even more test trials (32 vs. 96). This indicates long-lasting, extinction-resistant bidirectional associations.

Further, since the current paradigm is conceptually very close to that of Herwig and Horstmann (2011), and the adults failed to show frequency effects, it is more likely that in the manual version of the action–effect task of Verschoor *et al.* (2010), the action effects affected response choice differently from the current paradigm. In manual action–effect paradigms the only attention-drawing events in the test phase are the presented action effects. Their mere presence is unlikely to affect action choice directly, so that all possible response biases can be attributed to the degree to which the action effect reactivated a previously acquired association, which then spread activation to the corresponding response representation. In other words, even though action effects attract exogenous attention, they eventually impact action selection in an entirely endogenous fashion. Indeed, neuroimaging studies have shown that the presentation of previously acquired action effects activates the supplementary motor area, which underlies endogenously driven but not exogenously driven action selection (Elsner, Hommel, Mentschel, Drzezga, Prinz, Conrad & Siebner, 2002; Melcher, Weidema, Eenshuistra, Hommel & Gruber, 2008; Paulus *et al.*, 2011). In contrast, in our oculomotor version of the task, the

endogenous impact of the action effect competes with the direct, exogenous impact of the saccade goals – the faces in our case. It is possible that this exogenous impact is so strong that it outweighs the impact of the endogenous bias to a degree that the latter is too weak to determine which response is being chosen, even though it can still speed up congruent and/or slow down incongruent responses. Accordingly, the present findings do not necessarily require the assumption that action–effect learning is different in, or follows different developmental pathways with respect to, manual and oculomotor actions. One could even speculate that the exogenous attention evoked had a stronger impact on the 7-month-olds, thus resulting in a lack of RT effect in this group.

As expected, we found reliable effects of congruency on pupil dilation with incongruent saccades resulting in larger relative dilations. These findings need to be interpreted with caution, as there are no shared standards regarding the handling of TEPRs. TEPRs can start from 200–300 ms after stimulus onset and peak around 1200 ms post-stimulus (Beatty & Lucero-Wagoner, 2000), sometimes even later (e.g. Bradley *et al.*, 2008; Beatty, 1982). The effects found do fit within these temporal dynamics. On the other hand, little is known about developmental and aging-related changes in these biometric variables across the lifespan. Since our experiment is self-paced (to ensure infant cooperation) ITIs do vary systematically between age groups, with shorter ITIs for the adults. What is more, in the 12-month-olds and adults RTs also vary with congruency. These timing factors could reduce pupillary effects in these age groups. Unfortunately, due to the attentional abilities of infants standardizing the ITIs was not an option. Furthermore, since light adaptation dilations decrease in amplitude and latency with increasing gestational age (Cocker, Fielder, Moseley & Edwards, 2005), one could speculate that the same could hold true for TEPRs. Thus ideal intervals for measuring TEPRs and baselines may vary accordingly. Therefore, pupillary effects should be expected to be most pronounced in the 7-month-olds. This is indeed what we find. In the current study we chose intervals as suggested by the literature. However, in the literature there is no standard for response-related evaluative effects.

To accommodate for the variable RTs and ITIs in the current experiment, we considered both stimulus-locked and response-locked TEPRs, which, however, yielded identical outcomes. Of particular interest, both analyses revealed main effects of congruency but no interaction with age. Moreover, the congruency effects remained reliable when being tested in the 7-month-olds alone, the only age group that did not show a congruency effect in

RTs. On the one hand, the fact that 7-month-olds are sensitive to the congruency between their action and the presented action effect demonstrates that they have acquired information about the relationship between their actions and the novel auditory effects these actions produced in the experiment. Accordingly, we take this observation to indicate that even the youngest group was able to integrate some kind of information about actions and their effects. On the other hand, the dissociation between the dilation effect and the RT effect in these infants suggests that the two measures do not assess the same underlying processes.

As suggested by Band *et al.* (2009) and Blakemore, Frith and Wolpert (1999), action–effect associations may not only serve as an informational basis for action selection, the major theme of ideomotor theory, but also for predicting the perceptual consequences of an action. This prediction can be matched against the actually produced consequences in order to evaluate whether the action goal was reached. The late timing of our stimulus- and response-locked congruency effects in the TEPRs suggests that these effects were picking up processes related to action evaluation rather than action selection proper. Indeed, error-related negativity type patterns as reported by Band *et al.* (2009) in connection with action prediction have been found to be related to pupillary responses as well (Wessel, Danielmeier & Ullsperger, 2011). These pupillary effects might thus indicate a mismatch between expected and actual action effect in incongruent trials and/or reflect the adaptive processes thereby triggered that update the system's knowledge about action–effect relationships. The first possibility would fit well with the violation-of-expectation approach suggested by Jackson and Sirois (2009) and Gredebäck and Melinder (2010), while the interpretation in terms of mismatch-induced control processes would be more along the lines of the traditional TEPR literature – which focuses on arousal, attention allocation, cognitive load and mental effort. In any case, the effect reflects knowledge about action–effect contingencies, and our stimulus- and response-locked findings suggest that this knowledge is equally present in all three age groups.

This dissociation between RT findings, which imply action-selection effects in adults and 12-month-olds, and TEPRs, which suggest action-evaluation effects in all participants, allows for two important conclusions. First, the processing of an action–effect stimulus activates a representation that creates particular expectations, without necessarily activating the corresponding actions. This means that action–effect expectation may be correlated with, and perhaps even functional for, action selection (Kühn, Keizer, Rombouts & Hommel, 2011) in older agents, but raising an expectation is not identical to

selecting an action. Second, infants' abilities to construct action–effect expectations develop earlier than their abilities to use action–effect representation for intentional action selection. A similar dissociation between acquisition of action–effect knowledge versus use of action–effect knowledge was reported by Sommerville *et al.* (2005). They showed that violation-of-expectation to a change of goal was influenced by action–effect experience in 3-month-olds, while the observation of actions and their effects did not influence action production.

There are several possible reasons why selection abilities develop more slowly and why action–effect knowledge in the 7-month-olds affected expectation-related effects only. One possibility is that associations between motor patterns and novel action effects are either not yet bidirectional, are too weak, or take too much time to retrieve to affect performance under our testing conditions. Another possibility is that novel action effects are not yet directly associated with actions but only with representations of already existing action effects. Taken altogether, it seems safe to assume that, at 7 months of age, knowledge about relations between actions and their effects has a stronger impact on the prediction of action effects than on the selection of intentional actions.

To conclude, the dissociation we obtained in 7-month-olds suggests a developmental precedence of action monitoring over intentional action selection. This again suggests that infants acquire the knowledge necessary for performing intentional actions sometime before they have (fully) developed the cognitive machinery necessary to make use of that knowledge to perform intentional action (Keen, 2005; Sommerville *et al.*, 2005). Combining the current data with those of Verschoor *et al.* (2010) suggests a major change in action–effect learning from just action monitoring to action selection, just before the ninth month of age. If one takes into account the functional and representational equivalence of self-performed and perceived actions as suggested by Theory of Event Coding (Hommel *et al.*, 2001), this pattern fits with data suggesting that at 6 months of age infants can understand goal-directed action (e.g. Woodward, 1998), or more accurately, experience violation-of-expectation to a change of goal, but are unable to perform true intentional action (distinguishing means from ends) until around 8 to 9 months of age (Goubet, Rochat, Maire-Leblond & Poss, 2006; Hauf, 2007; Piaget, 1936, [1963]). Our findings also fit with results from studies on action perception, showing that infants at 9 but not 7 months of age can use observed action–effect relations to guide behavior (Hauf & Aschersleben, 2008). In addition, our data suggest that motor resonance when listening to

previously self-produced sounds in 8-month-olds, as found by Paulus *et al.* (2011), might indeed reflect the existence of knowledge about action–effect relations; and yet, we do not necessarily expect this knowledge to result in overt behavior, at least not at 7 months of age. Similar evidence for action–knowledge activation during action observation has been obtained in infants as young as 6 months (Nyström, 2008). Some authors have argued that it is lacking representational equivalence between self-produced actions and observed actions that prohibits infants younger than 9 months from imitation (Hauf, 2007). Our data, together with those of Paulus *et al.* (2011), Verschoor *et al.* (2010), Nyström (2008), and Sommerville *et al.* (2005), suggest that it is not representational equivalence that is reached by 9 months of age, but the ability to successfully use bidirectional action–effect associations, learned either by observation or by experience, for voluntary action.

Disclosure

The authors declare no competing interests.

Acknowledgements

This research was supported by the Netherlands Organization for Scientific Research. We especially thank Thijs Schrama for technical support and Henk van Steenbergen for analytical support.

References

- Baker, C.L., Saxe, R., & Tenenbaum, J.B. (2009). Action understanding as inverse planning. *Cognition*, **113** (3), 329–349.
- Band, G.P.H., van Steenbergen, H., Ridderinkhof, K.R., Falkenstein, M., & Hommel, B. (2009). Action–effect negativity: irrelevant action effects are monitored like relevant feedback. *Biological Psychology*, **82**, 211–218.
- Beatty, J. (1982). Task-evoked pupillary responses, processing load, and the structure of processing resources. *Psychological Bulletin*, **91**, 276–292.
- Beatty, J., & Lucero-Wagoner, B. (2000). The pupillary system. In J. Caccioppo, L.G. Tassinary & G. Berntson (Eds.), *The handbook of psychophysiology* (2nd edn., pp. 142–162). Cambridge: Cambridge University Press.
- Biro, S., & Leslie, A. (2007). Infants' perception of goal-directed actions: development through cue-based bootstrapping. *Developmental Science*, **10**, 379–398.
- Blakemore, S.-J., Frith, C.D., & Wolpert, D.W. (1999). Spatiotemporal prediction modulates the perception of

- self-produced stimuli. *Journal of Cognitive Neuroscience*, **11**, 551–559.
- Bradley, M.M., Miccoli, L., Escrig, M.A., & Lang, P.J. (2008). The pupil as a measure of emotional arousal and autonomic activation. *Psychophysiology*, **45**, 602–607.
- Cocker, K.D., Fielder, A.R., Moseley, M.J., & Edwards, A.D. (2005). Measurements of pupillary responses to light in term and preterm infants. *Neuro-Ophthalmology*, **29**, 95–101.
- Csibra, G. (2008). Goal attribution to inanimate agents by 6.5-month-old infants. *Cognition*, **107**, 705–717.
- Csibra, G., Gergely, G., Biro, S., & Koós, O. (1999). Goal attribution without agency cues: the perception of ‘pure reason’ in infancy. *Cognition*, **72**, 237–267.
- DeCasper, A.J., & Fifer, W.P. (1980). Of human bonding: newborns prefer their mothers’ voices. *Science*, **1208**, 1174–1176.
- Dutzi, I.B., & Hommel, B. (2009). The microgenesis of action–effect binding. *Psychological Research*, **73**, 425–435.
- Eenshuistra, R.M., Weidema, M.A., & Hommel, B. (2004). Development of the acquisition and control of action–effect associations. *Acta Psychologica*, **115**, 185–209.
- Elsner, B. (2007). Infants’ imitation of goal-directed actions: the role of movements and action effects. *Acta Psychologica*, **124**, 44–59.
- Elsner, B., & Hommel, B. (2001). Effect anticipation and action control. *Journal of Experimental Psychology: Human Perception and Performance*, **27**, 229–240.
- Elsner, B., & Hommel, B. (2004). Contiguity and contingency in action–effect learning. *Psychological Research*, **68**, 138–154.
- Elsner, B., Hommel, B., Mentschel, C., Drzezga, A., Prinz, W., Conrad, B., & Siebner, H.R. (2002). Linking actions and their perceivable consequences in the human brain. *Neuro-Image*, **17**, 364–372.
- Fabbri-Destro, M., & Rizzolatti, G. (2008). Mirror neurons and mirror systems in monkeys and humans. *Physiology*, **23**, 171–179.
- Falck-Ytter, T. (2008). Face inversion effects in autism: a combined looking time and pupillometric study. *Autism Research*, **1**, 297–306.
- Falck-Ytter, T., Gredebäck, G., & von Hofsten, C. (2006). Infants predict other people’s action goals. *Nature Neuroscience*, **9**, 878–879.
- Gergely, G., & Watson, J.S. (1999). Early social-emotional development: contingency perception and the social biofeedback model. In P. Rochat (Ed.), *Early social cognition* (pp. 101–136). Hillsdale, NJ: Erlbaum Publishers.
- Goren, C.C., Sarty, M., & Wu, P.Y. (1975). Visual following and pattern discrimination of face-like stimuli by newborn infants. *Pediatrics*, **56**, 544–549.
- Goubet, N., Rochat, P., Maire-Leblond, C., & Poss, S. (2006). Learning from others in 9- to 18-month-old infants. *Infant Child Development*, **15**, 161–177.
- Gredebäck, G., & Melinder, A. (2010). Infants’ understanding of everyday social interactions: a dual process account. *Cognition*, **114**, 197–206.
- Greenwald, A.G. (1970). Sensory feedback mechanisms in performance control: with special reference to the ideomotor mechanism. *Psychological Review*, **77**, 73–99.
- Harless, E. (1861). Der Apparat des Willens. *Zeitschrift fuer Philosophie und philosophische Kritik*, **38**, 50–73.
- Hartshorn, K., Rovee-Collier, C., Gerhardtstein, P., Bhatt, R.S., Wondolowski, T.L., Klein, P., Gilch, J., Wurzel, N., & Campos-de-Carvalho, M. (1997). The ontogeny of long-term memory over the first year-and-a-half of life. *Developmental Psychobiology*, **32**, 69–89.
- Hauf, P. (2007). Infants’ perception and production of intentional actions. *Progress in Brain Research: From Action to Cognition*, **164**, 285–301.
- Hauf, P., & Aschersleben, G. (2008). Action–effect anticipation in infant action control. *Psychological Research*, **72**, 203–210.
- Herwig, A., & Horstmann, G. (2011). Action–effect associations revealed by eye movements. *Psychonomic Bulletin & Review*, **18**, 531–537.
- Hess, E.H. (1975). *The tell-tale eye: How your eyes reveal hidden thoughts and emotions*. New York: Van Nostrand Reinhold.
- Hess, E.H., & Polt, J. (1960). Pupil size as related to interest value of visual stimuli, *Science*, **132**, 149–150.
- Hess, E.H., & Polt, J. (1964). Pupil size in relation to mental activity during simple problem-solving. *Science*, **13**, 1190–1192.
- Hommel, B. (1996). The cognitive representation of action: automatic integration of perceived action effects. *Psychological Research*, **59**, 176–186.
- Hommel, B., & Elsner, B. (2009). Acquisition, representation, and control of action. In E. Morsella, J.A. Bargh & P.M. Gollwitzer (Eds.), *Oxford handbook of human action* (pp. 371–398). New York: Oxford University Press.
- Hommel, B., Müsseler, J., Aschersleben, G., & Prinz, W. (2001). The theory of event coding (TEC): a framework for perception and action planning. *Behavioral and Brain Sciences*, **24**, 849–937.
- Hupe, J.M., Lamirel, C., & Lorenceau, J. (2009). Pupil dynamics during bistable motion perception. *Journal of Vision*, **9**, 1–19.
- Jackson, I., & Sirois, S. (2009). Infant cognition: going full factorial with pupil dilation. *Developmental Science*, **12**, 670–679.
- James, W. (1890). *The principles of psychology*. New York: Macmillan/Harvard University Press.
- Johnson, M.H., Dziurawiec, S., Ellis, H., & Morton, J. (1991). Newborns’ preferential tracking of face-like stimuli and its subsequent decline. *Cognition*, **40**, 1–19.
- Johnson, S.C., Ok, S.-J., & Luo, Y. (2007). The attribution of attention: 9-month-olds’ interpretation of gaze as goal-directed action. *Developmental Science*, **10**, 530–537.
- Kahneman, D. (1973). *Attention and effort*. Englewood Cliffs, NJ: Prentice Hall.
- Kahneman, D., & Beatty, J. (1966). Pupil diameter and load on memory. *Science*, **154**, 1583–1585.
- Keen, R. (2005). Using perceptual representations to guide reaching and looking. In J. Rieser, J. Lockman & C.A. Nelson (Eds.), *Action as an organizer of learning and*

- development: Minnesota Symposium on Child Psychology*, 33 (pp. 301–322). Mahwah, NJ: Lawrence Erlbaum Associates.
- Kiraly, I., Jovanovic, B., Prinz, W., Aschersleben, G., & Gergely, G. (2003). The early origins of goal attribution in infancy. *Consciousness and Cognition*, **12**, 752–769.
- Klein, A., Hauf, P., & Aschersleben, G. (2006). The role of action effects in 12-month-olds' action control: a comparison of televised model and live model. *Infant Behavior and Development*, **29**, 535–544.
- Kray, J., Eenshuistra, R., Kerstner, H., Weidema, M., & Hommel, B. (2006). Language and action control: the acquisition of action goals in early childhood. *Psychological Science*, **17**, 737–741.
- Kühn, S., Keizer, A., Rombouts, S.A.R.B., & Hommel, B. (2011). The functional and neural mechanism of action preparation: roles of EBA and FFA in voluntary action control. *Journal of Cognitive Neuroscience*, **23**, 214–220.
- Laeng, B., & Falkenberg, L. (2007). Women's pupillary responses to sexually significant others during the hormonal cycle. *Hormones and Behavior*, **52**, 520–530.
- Laeng, B., Sirois, S., & Gredebäck, G. (2012). Pupillometry: A window to the preconscious? *Perspectives on Psychological Science*, **7**, 18–27.
- Libby, W.L., Lacey, B.C., & Lacey, J.I. (1973). Pupillary and cardiac activity during visual attention. *Psychophysiology*, **10**, 270–294.
- Lotze, R.H. (1852). *Medicinische Psychologie oder Physiologie der Seele*. Leipzig: Weidmann.
- Melcher, T., Weidema, M., Eenshuistra, R.M., Hommel, B., & Gruber, O. (2008). The neural substrate of the ideomotor principle: an event-related fMRI analysis. *NeuroImage*, **39**, 1274–1288.
- Meltzoff, A.N. (2006). The 'like me' framework for recognizing and becoming an intentional agent. *Acta Psychologica*, **124**, 26–43.
- Meltzoff, A.N., & Moore, M.K. (1997). Explaining facial imitation: a theoretical model. *Early Development and Parenting*, **6**, 179–192.
- Meltzoff, A.N., & Prinz, W. (Eds.) (2002). *The imitative mind: Development, evolution and brain bases*. Cambridge: Cambridge University Press.
- Miltner, W.H.R., Braun, C.H., & Coles, M.G.H. (1997). Event-related potentials following incorrect feedback in a time-estimation task: evidence for a 'generic' neural system for error detection. *Journal of Cognitive Neuroscience*, **9**, 788–798.
- Nyström, P. (2008). The infant mirror neuron system studied with high density EEG. *Social Neuroscience*, **3** (3–4), 334–337.
- Paulus, M., Hunnius, S., Elk, M., & Beckering, H. (2012). How learning to shake a rattle affects 8-month-old infants' perception of the rattle's sound: electrophysiological evidence for action–effect binding in infancy. *Developmental Cognitive Neuroscience*, **2** (1), 90–96.
- Perra, O., & Gattis, M. (2010). The control of social attention from 1 to 4 months. *British Journal of Developmental Psychology*, **28**, 891–908.
- Piaget, J. (1936 [1963]). *The origins of intelligence in children*. New York: W.W. Norton & Company.
- Piaget, J. (1954). *The construction of reality in the child*. New York: Basic Books.
- Prinz, W. (1990). A common coding approach to perception and action. In O. Neumann & W. Prinz (Eds.), *Relationships between perception and action* (pp. 167–201). Berlin: Springer.
- Prinz, W. (1997). Perception and action planning. *European Journal of Cognitive Psychology*, **9**, 129–154.
- Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annual Review of Neuroscience*, **27**, 169–192.
- Rochat, P. (2001). *The infant's world*. Cambridge, MA: Harvard University Press.
- Rochat, P., & Striano, T. (1999). Emerging self-exploration by 2-month-old infants. *Developmental Science*, **2**, 206–218.
- Rovee, C.K., & Rovee, D.T. (1969). Conjugate reinforcement of infant exploratory behavior. *Journal of Experimental Child Psychology*, **8**, 33–39.
- Rovee-Collier, C. (1999). The development of infant memory. *Current Directions in Psychological Science*, **8**, 80–85.
- Scerif, G., Karmiloff-Smith, A., Campos, R., Elsabbagh, M., Driver, J., & Cornish, K. (2005). To look or not to look? Typical and atypical development of oculomotor control. *Journal of Cognitive Neuroscience*, **4**, 591–604.
- Schneider, W., Eschman, A., & Zuccolotto, A. (2002). *E-Prime user's guide*. Pittsburgh, PA: Psychology Software Tools Inc.
- Senju, A., & Csibra, G. (2008). Gaze following in human infants depends on communicative signals. *Current Biology*, **18**, 668–671.
- Snodgrass, G., & Vanderwart, M. (1980). A standardized set of 260 pictures: norms for naming agreement, familiarity, and visual complexity. *Journal of Experimental Psychology: Human Learning and Memory*, **6**, 174–215.
- Sommerville, J.A., Woodward, A.L., & Needham, A. (2005). Action experience alters 3-month-old infants' perception of others' actions. *Cognition*, **96**, B1–B11.
- Tomasello, M. (1999). *The cultural origins of human cognition*. Cambridge, MA: Harvard University Press.
- Verschoor, S., & Biro, S. (2012). Means selection information overrides outcome selection information in infants' goal attribution. *Cognitive Science*, **36**, 714–725.
- Verschoor, S.A., Weidema, M., Biro, S., & Hommel, B. (2010). Where do action goals come from? Evidence for spontaneous action–effect binding in infants. *Frontiers in Cognition*, **1**, 201.
- von Hofsten, C. (2004). An action perspective on motor development. *Trends in Cognitive Sciences*, **8**, 266–272.
- Watson, J.S. (1967). Memory and 'contingency analysis' in infant learning. *Merrill-Palmer Quarterly*, **13**, 55–76.
- Wessel, J.R., Danielmeier, C., & Ullsperger, M. (2011). Error awareness revisited: Accumulation of multimodal evidence from central and autonomic nervous systems. *Journal of Cognitive Neuroscience*, **23**, 3021–3036.
- Woodward, A. (1998). Infants selectively encode the goal object of an actor's reach. *Cognition*, **69**, 1–34.
- Woodward, A.L. (2009). Infants' grasp of others' intentions. *Current Directions in Psychological Science*, **18**, 53–57.

Received: 31 August 2011

Accepted: 26 March 2013