Neural representations of grasp congruence during the emergence of precision grasping

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Abstract

Grasping is a fundamental skill that enables people to interface with and explore objects around them. The emergence of precision (thumb-to-forefinger) grasping during infancy represents a developmental shift in this skill and has been linked to more advanced action perception, particularly in detecting action incongruencies. In this study, ERPs known to be elicited in response to action were studied in 9- and 11.5-month-old infants as they watched whole-hand and precision grasping actions congruent or incongruent with a target object. Components related to attentional (Nc, P400) and semantic (N400) processes were examined to determine whether infants' perception of grasp is based on attention and recognition, on higher-level representations of action, or a mix of these two levels of processing. Effects of congruence were found for the P400 and the N400. The P400 effect was greater among the older age group. Infants' ability to produce a precision grip did not significantly affect their ERPs in response to actors' incongruent versus congruent grasps, which would have been expected if recognition of incongruous grasping actions were based on motor experience. Results indicate that infant ERPs differ between grasps that are congruent or incongruent with the form of a target object via multiple cognitive processes.

Keywords: Action, infancy, ERP, N400, P400

Introduction

The emergence of functional object use in infancy signals a convergence of motor and cognitive skills. Appropriate use of an object requires that multiple mental representations are accessed - the object must be associated with a specific target or category of targets; there must be a representation of what the object does to that target (its function); and there must be a representation of how to manipulate the object to achieve that function (van Elk et al., 2010). Infants by the end of the first post-natal year associate functional objects with targets (Hunnius & Bekkering, 2010) and mentally represent the effects of using specific tools (Hernik & Csibra, 2015; Träuble & Pauen, 2011). One step towards learning how to manipulate objects is representing their motor affordances. Around six months of age, infants begin to do this, for example forming expectations about how to grasp objects of different shapes (Daum et al., 2009). The ability to form and use thumb-to-finger (or precision) grips has been positively related to the ability to predict how another person will grasp an object (Daum et al., 2011; Loucks & Sommerville, 2012). The aim of the present study was to examine the neural correlates of the perception of others' grasping behaviour, with a secondary focus on the effect of infants' own grasping ability.

The emergence of precision grasping

Grasping is an early-developing, object-directed action with a clear goal or end-state, which makes it ideal as an exemplar for action perception research. The nature of grasping changes throughout infancy, which means that different types of grasping actions can be used to examine how infants' own motor abilities affect their perception of other people's actions (e.g. Daum et al., 2009, 2011; Loucks & Sommerville, 2012). One key transition in grasping behaviour is learning to pick things up using the index

finger and thumb, a motor milestone typically reached by twelve months of age according to multiple health authorities³. This ability is known as the precision grip, and is contrasted with the power grip in which an object is "forcefully clamped between the under-surface of the fingers and the palm of the hand" (Butterworth et al., 1997, p.223).

Precision and power grips are superordinate categories. Analysis of grasping behaviour has often been more granular. For example, Halverson (1931/1975) described infant grasping behaviour according to ten categories, from touching (or not touching) a target object, through using the hand to squeeze or rake the object towards oneself, to grasping it with the palm and eventually with the forefinger and thumb. Touwen (1971) used five sub-categories including palmar grips, radial palmar grips (which include thumb opposition), scissor grips, scissor-pincer grips, and pincer grips, with the latter three covering the transition from using the inner surfaces of the digits to hold an object, to using the tips of index finger and thumb. Butterworth and colleagues (1997) drew on these earlier works in identifying four sub-categories each of power and precision grips.

Before precision grasping emerges, the infant first learns to use active thumb opposition, with Halverson (1931/1975) noting a "simultaneous budding into prominence" (p. 217) of the forefinger alongside the thumb. This in turn leads to more advanced prehension like precision grasping. Halverson (1931/1975) identified that this ability emerges between approximately six and eight months of age. Touwen (1971) reported a range of five to nine months for the onset of the radial palmar grip.

³Health Service Executive, Ireland, <u>https://www2.hse.ie/babies-children/checks-milestones/developmental-milestones/7-12-months/</u>; Centers for Disease Control and Prevention, USA, <u>https://www.cdc.gov/ncbddd/actearly/milestones/milestones-1yr.html</u>; National Health Service, UK, https://cambspborochildrenshealth.nhs.uk/child-development-and-growing-up/milestones/12-months/

Butterworth et al. (1997) found that the power grip most favoured by six- to eightmonth-olds was the hand grasp, which does not require thumb opposition. By 12 to 14 months, the radial palm grasp was the most frequently-used power grip.

For Halverson (1931/1975), the subsequent transition from using the palm to using the digits independently was a key juncture, signalling the emergence of the precision grip. While some infants in his sample showed this ability at 32 weeks of age (approximately 7.5 months), only at 36 weeks (8.5 months) were precision grips used more than power grips. Touwen (1971) reports precision grip emergence from as early as seven months to as late as 11 months. Butterworth and colleagues (1997) found a decrease in power grip use and a yoked increase in precision grip use with age, particularly between the six- to eight- and nine- to 11-month-old age groups. These results suggest that infants begin to use precision grips in the latter half, and typically the latter third, of the first year.

Effects of precision grasping on action perception

Although the distinction between types of grasping in this literature has been granular, comparing infants' action perception on the basis of grasping ability has often required a binary distinction between precision graspers and non-precision graspers. For example, Daum and colleagues (2009; 2011) examined infants' preference for looking at a grasping outcome that matched or didn't match the hand shape used in the preceding action. Specifically, a hand was shown reaching behind an occluder with the thumb held opposite the fingers, with either a wide or narrow gap between the thumb and fingers. Subsequently, they compared infants' looking to images with the occluder removed and either the wide-shaped hand holding the side of a mug, or the narrow-shaped hand holding its handle. They found longer looking times to the

mismatched, or unexpected, action end-state in both six- and nine-month-old infants (Daum et al., 2009).

They also examined whether six-month-olds could grasp a small object with thumb opposition, using the four precision grip subcategories from Butterworth et al. (1997) as well as one of the power grip subcategories (radial palm grasp) in which the thumb is used in opposition to the index finger (Daum et al., 2011). Six-month-olds who used thumb opposition looked longer at the unexpected outcome; those who did not use thumb opposition looked equally long at each outcome. While not a perfect reflection of the motor distinction in the stimuli, in which thumb opposition was always present, these results show how the progression of infants' grasping ability alters how they encode other people's object-related actions.

Another example comes from Loucks and Sommerville (2012) who found that 10-month-olds who used a precision grip to retrieve a toy from a small container were sensitive to both the type of grip (whole-hand⁴ versus precision) used by another person, and to whether that grip was functional for picking up a target object. Those who did not engage in precision grasping were sensitive only to the type of grip. This body of work indicates how infants' ability to physically manipulate objects affects their perception of others' actions. In the present study, we employed event-related potentials (ERPs) to investigate infants' encoding of other people's grasping actions, and the relation to infants' own precision grasping ability.

Infant action-related ERPs

Three infant ERPs were investigated – the Nc, N400 and P400. Each is involved in the processing of action, sometimes manifesting differently between the middle of the

⁴Note the use of "whole-hand" rather than power grasp by the original authors. This is due to the palm not being used in the non-functional whole-hand grasping action.

first postnatal year and the beginning of the second postnatal year. The first component, the Nc, is generally thought to index whether the infant has focused attention more strongly on a stimulus (Nelson, 1994; Reynolds & Richards, 2019), for example when a stimulus from a novel category is seen (Quinn et al., 2006). Occurring around 300 to 600 ms after stimulus onset, the Nc is typically larger in response to novel than familiar actions (Carver et al., 2000; Monroy et al., 2019), although in some cases there is a familiarity effect (e.g. for eating actions, Kaduk et al., 2016; Reid et al., 2009).

The N400 component is also seen in response to actions but is elicited by semantic violations rather than attention. For example, in adults, an N400 is elicited by actions performed with an inappropriate context or tool (Amoruso et al., 2013; Bach et al., 2009; Proverbio & Riva, 2009; Sitnikova et al., 2008). An N400 is elicited when infants observe incongruous actions (e.g. placing food on the forehead instead of in the mouth; Kaduk et al., 2016; Reid et al., 2009). The latency and topography of the infant N400, even in word-learning contexts, have been variably defined (Junge et al., 2021), though in action contexts it is usually a mid-latency (e.g. 600 ms at nine months) component that manifests over posterior electrodes (Kaduk et al., 2016; Monroy et al., 2019; Pace et al., 2013; Reid et al., 2009).

The P400 has a similar latency to the Nc but manifests via a more posterior topography. It is part of an N290-P400 complex, associated with face processing and thought to be homologous to the adult N170 (de Haan et al., 2003). It has also been found in response to referential actions such as gaze (Senju et al., 2006) and pointing (Gredebäck et al., 2010; Melinder et al., 2015), and thus may be involved in detecting relevant, often social, information. In a study with six-month-olds by Bakker and colleagues (2015), the P400 ERP component was elicited differently when a hand in

grasping posture was directed towards or away from an object's location. It was found in younger infants who could use power grasps (Bakker et al., 2015) and had received "sticky mittens" grasp training (Bakker et al., 2016). These authors speculate that the P400's role in action may be to relate motor experience to observed actions.

The present study

Much of the literature on infant action perception has focused on the end states or goals of actions, which even five-or six- month-old infants detect (Hunnius & Bekkering, 2010; Luo & Baillargeon, 2005; Woodward, 1998). Indeed, infants can learn the functions of objects even if they cannot yet use them (Elsner & Pauen, 2007). As infants develop the ability to use grasped objects as tools (for example, through self-feeding with spoons or cups), they become sensitive to how objects or tools are grasped and whether this matches the object (Daum et al., 2009; 2011) or facilitates further action (Ní Choisdealbha et al., 2016; Paulus et al., 2011). Whereas prior ERP work has focused on the end state, or goal, of an action (Reid et al., 2009; Kaduk et al., 2016), here we examine how infants encode how actions are performed. For each of the components in question, goal-directed actions elicit larger versions of these components when they are novel or unexpected. We therefore expected to find that they differ for congruent and incongruent grasps on familiar objects.

The investigation of these components was the primary aim of this work, as they each relate to different aspects of early action processing. However, based on related work, we investigated two additional questions. The first was the effect of age. The previous work showed that the P400 response is present at six months of age (Bakker et al., 2015), and the goal-related Nc response is present at seven months (Reid et al., 2009). The N400 for actions emerges later, from nine months (Reid et al., 2009; Kaduk et al., 2016). However, the effects in these studies were found in

response to a familiar action goal (putting food in the mouth). This kind of direct goal perception develops early, for example Woodward (1998) showed that infants anticipate an actor's goal by five months, and Hunnius and Bekkering (2010) showed that six-month-olds will make anticipatory looks to the target areas of common actions (e.g. looking to the mouth when an actor is holding a cup).

Conversely, encoding and responding to the affordances of how an object is grasped are later-developing abilities (some but not all infants can do these things by 6 months, Daum et al., 2011), and consequently we might expect ERP responses differentiating actions on the basis of grasp type (versus grasp direction, Bakker et al., 2015) to emerge later. A nine-month-old target age group was selected on the basis that all three of these components are present, at least for goal perception. An 11.5-month-old comparison group was selected to find if the components changed over a period in which infants become more experienced with precision grasping (Butterworth et al., 1997; Halverson, 1931/1975). Reid and colleagues (2009) found a developmental shift in their investigated components over a two-month period, with the Nc being present at first and the N400 emerging later. We examined the same, shifting the target ages slightly older on the assumption that the ability to distinguish actions on the basis of *means*, or the type of grasp used, would be a later emerging ability than distinguishing actions on the basis of *goals*, or target location.

The second additional question, as highlighted earlier relates to the infants' own action production. Bakker and colleagues (2015) found that proficient five-month-old graspers showed a difference in their P400 response to grasping actions relative to their less proficient peers. They also found that when presented with hands in a precision grip posture rather than a power grip posture, six-month-olds did not show a difference in the P400 response, suggesting that experience is necessary to encode

functional differences in hand shape. Consequently, as well as studying infants' responses to precision and whole-hand grasps that were congruent or incongruent with a target object, we also measured infants' grasping ability to examine its effects on their encoding of others' grasping actions. We anticipated thatinfants who performed precision grips would show a greater difference in their ERPs to others' congruent and incongruent grasping actions. Although we measured grasping via multiple items, ultimately we narrowed these down to execution of a precision grip as a predictor of action encoding via ERP measures. This reflects the key difference between the grasping actions displayed to the infants, and thus the effects of motor experience on action encoding should be reflected in their ability to perform this grip.

Methods

Participants

Participants were recruited from the research participant pool of an infant research centre in north-west England. The study received approval from the ethics committee of the Department of Psychology at the Lancaster, was conducted in line with the Declaration of Helsinki with written informed consent obtained from a parent or guardian for each infant before any assessment or data collection. Individual demographic data were not collected due to data protection regulations. The local population from which the sample was recruited is 93.1% white, 3.6% Asian, 1% Black, and 1.5% of mixed or multiple ethnic groups (UK Census 2021). The local area ranks in the 35th percentile for income deprivation among English local authorities.

The samples of 30 nine-month-olds (16 boys) and 26 11.5-month-olds (nine boys) were tested consecutively. The first group had a mean age of nine months and three days (standard deviation (SD) = 11.5 days; date of birth missing for two infants),

and ranged from eight months, 13 days to nine months, 24 days. The second had a mean age of 11 months and 24 days (SD = 8.2 days), from 11 months, eight days, to 12 months, seven days. Demographic information was not collected due to data protection requirements surrounding personal data. Six nine-month-olds and two 11.5-month-olds were excluded from the EEG analyses for experimenter error (n = 1), technical issues (n = 3), and refusal to tolerate the EEG cap (n = 4). Of these babies, the four who did not tolerate the EEG cap and one who experienced technical issues did not take part in the subsequent behavioural measures. Two additional 11.5-month-olds were excluded at later stages of data processing (see Analysis section for details). Families received travel remuneration and a book in return for their participation.

Sample sizes were based on a similar research paradigm (Reid et al., 2009) but doubled due to an anticipated smaller effect size of grasp differences versus goal differences. Sensitivity analyses for multilevel regression are not trivial to perform. In lieu, equivalent single level multiple regression models were run, and relevant sensitivity analyses were run in G*Power 3.1 (Faul et al., 2007). Observed effect sizes exceeded the critical values of the sensitivity analyses (see Supplementary Materials).

Stimuli

Stimuli depicted female actors reaching for a cup with or without handles. Other research has employed cups with prior work showing that infants predict the outcomes of actions using cups (Hunnius & Bekkering, 2010) and detect object-grasp match (Daum et al., 2009; 2011). The action of reaching for and grasping the cup was performed on all cups by three female actors. Actions were presented in three static images to capture a clear, event-related response to the final grasping posture (Reid et al., 2009, Domínguez-Martinez et al., 2015). In the first image, each actor sat with her hands hidden below the table and the cup in front of her. In the second, she used

her right hand to reach, concealing the thumb to prevent any hand aperture cues that might generate expectations about the grasp.



Figure 1: Examples of the critical grasp stimulus across all conditions of congruence and grasp type. Handled and non-handled cups were shown in two colours, blue and yellow.

In the final image in each sequence, the actor grasped the cup with either her whole hand or with thumb-finger opposition, congruently or incongruently with the cup's shape (Figure 1). Neither incongruent grasp prevents use of the cup. There may arguably be differences in how commonly the incongruent whole-hand and precision grasps might be seen on comparable objects in daily life. However, pilot testing of the stimuli with 21 adults to check if an N400 effect was present in an adult population – which can be assumed to have developed robust grasping perception and production skills – found an effect of congruence but neither an effect of grasp nor a grasp-congruence interaction (see Supplementary Material). For this reason, and due to the difficulty of obtaining sufficient ERP data from infants for more than two experimental

conditions (Hoehl & Wahl, 2012), this study was undertaken with infants with the intention of contrasting congruence conditions only, though all grasp types were shown to maximise variety between the stimuli.

Procedure

Participants' neural responses to the stimuli were collected using an EGI 128-sensor geodesic Hydrocel sensor net (Electrical Geodesics Inc., Oregon). Data were recorded via an EGI NA300 amplifier using EGI Netstation software, and re-referenced online to Cz. Stimuli were presented using Matlab (TheMathworks, Inc., Massachusetts) with Psychtoolbox (Kleiner et al., 2007). Participants viewed the stimuli on a 20-inch CRT monitor (refresh rate 60 Hz) while sitting on their caregiver's lap approximately 50cm from the screen. At this distance, the visual angle of the cup was 15 by 12 degrees; the entire scene was 53 by 33 degrees. A video camera was used to record the infant during the experiment to determine if they saw the stimulus.

Within each sequence, the first two images were displayed for pseudorandomly determined durations of 0.8 to 1.2 s (in steps of 100 ms). The final image was displayed for 1 s. A white fixation cross appeared between sequences, in the same location as the cup. Sequences were pseudorandomly selected within Matlab with the rule that the same congruence, the same grasp, and the same actor and cup colour could not be shown more than twice in a row. The experiment ended when the infant became inattentive, fussy, or upset. Nine-month-olds were shown an average of 61.9 trials (SD = 11.8) and 11.5-month-olds were shown 50.7 trials (SD = 21).

Grasping ability has been measured in related work in various ways, including binary classification of a thumb-opposite or power grasp (Daum et al., 2009), ability to functionally use a precision grasp (Loucks & Sommerville, 2012), or a three-point

scale indicating non-attempts, non-successful attempts and successful grasps (Bakker et al., 2015). For this study, we include a binary measure of whether the infant used the pads of their fingertips to grasp a small pellet. This task was presented as part of a larger battery of tasks adapted from a developmental scale that was institutionally available (the Bayley Scales of Infant Development, BSID-II; Bayley, 1993). These tasks were performed in a separate room, after the EEG experiment had ended and the EEG cap was removed. Infants sat on their parent's lap at a small table opposite the experimenter who presented the items to be grasped (see Supplementary Materials for further details). Videos from ten randomly selected infants were coded by a second scorer naïve to the purpose of the study, for a total of 60 double-coded items reflecting the entire battery of items including precision grip production. Agreement between scorers was 90%, with a Cohen's kappa score indicating substantial agreement, $\kappa = 0.77$.

EEG processing

Videos of EEG sessions were coded for whether the infant was looking at the screen for the second and third images in each sequence. If not, the trial was marked for exclusion. A randomly selected group of eleven infants (six nine-month-olds, five 11.5month-olds; approximately 20% of the sample) was double-coded. Inter-rater agreement according to the Cohen's kappa score was high, $\kappa = 0.82$, with raters agreeing on 90.9% of the 617 double-coded trials. Data were exported from Netstation and imported into the EEGlab toolbox for Matlab (Delorme & Makeig, 2004). Files not originally recorded at 250Hz were downsampled from 1kHz, and then all files were processed using the HAPPE pipeline version 3 (Gabard-Durnam et al., 2018) as an ERP paradigm. The cleanline tool (Mullen, 2012) was used to reduce line noise (50Hz). Data were filtered using a Butterworth filter with a high-pass of 0.5 and a low-

pass of 45Hz. HAPPE defaults for bad channel rejection and wavelet thresholding were used. EEG epochs were segmented between -200ms and 1000ms from stimulus onset and baseline corrected from -200ms to stimulus onset. Automatic epoch rejection was based on both amplitude (thresholds of -500µV and 500µV) and similarity. The data were rereferenced to the average of the whole head. Subsequently, trials marked for exclusion based on the video recordings were removed using custom code and the EEGlab pop_select function.

After data were cleaned, there were on average 9 congruent trials (SD = 4.85) and 9.38 incongruent trials (5.28) remaining for nine-month-olds, and 10.21 (5.72) and 8.88 (5.29) respectively for the older group. For infants with sufficient trials for inclusion (eight per condition), these numbers were 9.63 (4.55) congruent and 9.38 (5.28) incongruent trials from nine-month-olds, and 11.05 (5.19) congruent and 9.68 (4.73) incongruent from 11.5-month-olds. The threshold of three trials was selected on the basis of research suggesting that, in a standard infant visual paradigm targeting the Nc or N400 component, three to seven trials are needed to obtain an interpretable ERP (Kaduk et al., 2016; Stets and Reid, 2011). Mean amplitudes for the Nc, N400 and P400 windows were calculated by averaging the amplitude values for each time point and electrode relevant to that component. Datapoints were excluded if they were more than 3.5 standard deviations greater or less than the mean amplitude for that component.

Electrode groups and time windows (Table 1) were selected on the basis of prior literature. The Nc time window and electrodes are the same as in Kaduk and colleagues' paper (2016). The N400 electrodes were taken from the same paper but the time window here is shifted 100ms earlier due to an expected earlier latency for this older sample (Junge et al., 2021; note that across studies, earlier N400 onsets are

used as sample ages get older). The P400 time window and electrodes were taken from Bakker and colleagues (2015), however, the offset was reduced by 100ms to avoid overlap with the N400 given their topographical proximity. The age group studied here is also older than that studied by Bakker and colleagues (2015). A common electrode group could have been used for both the N400 and P400 components but for the sake of comparability with prior literature, we adhered to the electrodes chosen by the authors of the prior work.

Component	Rol	Electrodes (EGI Hydrocel 128-	Time window
		channel net)	
Nc	Left and right	Left: 29, 30, 35, 36, 37, 40, 41,	300 to 600ms post-
	central	42, 46, 47	stimulus
		Right: 87, 93, 98, 102, 103, 104,	
		105, 109, 110, 111	
P400	Left and right	Left: 63, 64, 65, 67, 68, 69	300 to 500ms post-
	posterior	Right: 74, 75, 81, 86, 87, 88	stimulus
	temporal		
N400	Parietal	50, 51, 56, 57, 58, 59, 60, 65, 70,	500 to 700ms post-
		75, 76, 83, 84, 89, 90, 94	stimulus

Table 1:	Time	windows	and	electrode	es per	component
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Analysis

Data were analysed using linear mixed effects models via the ImerTest package in R (Kuznetsova et al., 2017), one analysis per component. For the Nc and P400 analyses,

fixed factors of age group, condition, hemisphere, precision grip production, and their interactions were included, with the exception of interactions involving both hemisphere and precision grip, for which there were no specific predictions. For the N400 component, the same model specification was used without the hemisphere factor. The models have one row per included trial, and participant identity was included as a random intercept.

Two 11.5-month-olds were excluded for contributing fewer than three clean trials in both conditions, resulting in a final sample of 24 nine-month-olds and 22 11.5-month-olds who contributed data to the analyses. Of these, there were 11 nine-month-olds and 14 11.5-month-olds who produced precision grips, and 14 and eight infants respectively who did not. Two nine-month-olds contributed data for incongruent trials only, due to having fewer than three clean congruent condition trials.

Results

The initial Nc multilevel model fit to the data was not significantly better than that of the random effects-only model ($\chi^2(11) = 19.377 \ p = 0.055$). Consequently, the model was simplified by dropping the three-way interaction between congruence, age, and precision grip production, after which the fit was better than the random effects-only model ($\chi^2(10) = 19.33$, p = 0.036). Tests of fixed effects showed a significant contribution to the model of hemisphere (F(1,1730.61) = 5.044, p = 0.025) and of the hemisphere by age interaction (F(1, 1730.61) = 4.204, p = 0.04), but no effects relating to congruence (see Table S2 in Supplementary Materials). Model estimates show that the Nc was generally more pronounced (more negative in amplitude) over the left than right hemisphere ($\beta = -2.392$, SE = 0.818, p = 0.011) and for the nine-month-olds relative to the older infants ($\beta = -2.392$, SE = 0.944, p = 0.012). The interaction

between age and hemisphere reflects the pattern seen in Figure 2, in which the leftright Nc difference is less pronounced at nine months than at 11.5 months (β = 2.592, SE = 1.14, *p* = 0.023). The crucial factor of congruence (relative to incongruence, β = -0.138, SE = 0.941, *p* = 0.884) and the congruence by precision grip performance interaction (congruent condition by precision grip performance, β = -0.588, SE = 0.814, *p* = 0.47) did not affect Nc amplitude. The beta coefficients of the are reported in full in the Supplementary Materials (Table S3).



Figure 2: Nc ERP wave forms from left and right central electrodes, plotted by age group. Responses to congruent stimuli are plotted in blue, incongruent in red. The shaded area denotes standard error of the mean. The vertical black lines indicate the analysed time window.



Figure 3: P400 ERP wave forms from left and right central electrodes, plotted by age group. Responses to congruent stimuli are plotted in blue, incongruent in red. The shaded area denotes standard error of the mean. The vertical black lines indicate the analysed time window. The N290 component, which typically occurs with the P400, can be seen just before or overlapping with the vertical line at 300ms.

The P400 model outperformed a random effects-only model ($\chi^2(11) = 20.047$, p = 0.045). Tests of fixed effects showed significant contributions of congruence (F(1, 1758.82) = 5.478, p = 0.019) and the congruent by age interaction (F(1, 1758.82) =

4.472, p = 0.035) to the model. P400 amplitude was affected by congruence, with a more positive amplitude for the incongruent than the congruent stimulus ($\beta = 3.888$, SE = 1.94, p = 0.045). It was also affected by age, with a more positive P400 component overall at nine than 11.5 months ($\beta = 4.59$, SE = 2.101, p = 0.03). There was an age by congruence interaction ($\beta = -6.818$, SE = 2.67, p = 0.011), indicating that the difference in congruence conditions was less evident for the nine-month-olds than for the older infants. There were no effects or interactions involving hemisphere (see Supplementary Materials, Table S4). The interaction between congruence and precision grip was non-significant (p = 0.76) as was the three-way interaction between congruence, age, and precision grip production (p = 0.09; beta estimate descriptively shows a larger incongruent P400 response among nine-month-olds who can perform a precision grip, $\beta = 4.951$, SE = 2.96, p = 0.094).

Finally, the N400 model performance did not exceed an equivalent random effects-only model ($\chi^2(7) = 13.902$, p = 0.053). However, simplifying the model by removing the three-way interaction did not improve model fit ($\chi^2(6) = 11.929$, p = 0.064) so we use the originally-specified model. The tests of fixed effects showed significant contributions of congruence (F(1, 884) = 5.051, p = 0.025) and of the age by precision grip performance interaction (F(1, 884) = 3.998, p = 0.046). The beta estimate for the effect of congruence indicates that it is the congruent stimulus which elicits a more negative N400 response ($\beta = -3.718$, SE = 1.465, p = 0.011). This congruence effect is opposite to the typical N400 effect, as it shows a larger (more negative) N400 in response to the congruent than the incongruent stimulus. The apparent difference by age in Figure 4, in which the congruent and incongruent N400 components appear different at 11.5 but not nine months, is likely explained by the marginal interaction between the congruent stimulus and the nine-month age group ($\beta = 3.763$ SE = 1.971,

p = 0.057). However, this is not an interaction which contributed significantly to model fit (p = 0.135).



Figure 4: N400 ERP wave forms plotted by age group. In the top row, responses to congruent stimuli are plotted in blue, incongruent in red. The bottom rows splits ERPs by the infant's demonstrated grip production, with those who produced a precision grip in blue and those who did not in red. The shaded area denotes standard error of the mean. The vertical black lines indicate the analysed time window. Note that the P400 peak is also evident over these electrodes at around 400ms post-stimulus.

The age by precision grip performance effect is explained by a negative estimate for the nine-month age group (β = -2.821, SE = 1.396, *p* = 0.044) and a positive estimate for the nine-month, precision grasping group (β = 4.417, SE = 1.855, *p* = 0.018). As suggested by Figure 4, the more negative N400 morphology is seen for non-precision graspers at nine months and for precision graspers at 11.5 months. Table S5 in the Supplementary Materials presents the full model results. Based on visual inspection of the waveforms in Figure 4, one could potentially argue for a later window matching that of previous work (600-800ms; Kaduk et al., 2016; Reid et al., 2009). Research on the infant action perception N400 is relatively limited (Pace et al., 2013; Kaduk et al., 2016; Michel et al., 2017; Monroy et al., 2019; Reid et al., 2009); further work may be required to support a systematic review similar to that conducted for the infant word-related N400 (Junge et al., 2021).

Discussion

Results indicate that infants' neural responses to grasping actions differentiate between grasps that are congruent and incongruent with the object upon which they are enacted. Effects were seen in the time windows and electrode groups for the P400 and N400 components, although not the Nc. This suggests that the processes involved in infants' differentiation of grasp-object "fit" are based on recognition of grasp appropriateness from experience, and on semantic processing of grasp function or purpose, with no effects founds for attentional orienting to more or less familiar stimuli. We did not find that infants who demonstrated a precision grip showed a greater distinction in their neural response to congruent and incongruent actions, which would have been expected if motor ability has a direct effect on action processing as reflected

in these ERPs. However, in order to draw firmer conclusions on this point, a larger sample size may be required. Secondary, exploratory analyses using a grasping score derived from multiple measures suggest that nine-month-olds with higher grasping scores show a greater congruence-related difference in N400 and P400 relative to peers with lower grasping ability (see Supplementary Materials, section "Analyses using granular grasping score"), suggesting that general manual motor ability rather than binary precision grip use may be a suitable production measure for future work.

Although an Nc peak was present in the ERP waveforms (with the exception of the 11.5-month-olds' right hemisphere electrodes), there was no effect of grasp congruence on the Nc. Previous research has shown that infants around the ages examined in the present study exhibit a larger Nc in response to actions that violate predictions (Monroy et al., 2019), and also to congruent food-related actions (Kaduk et al., 2016; Reid et al., 2009). These results are taken to mean that infants allocate more attention to such stimuli. In this study, it may have been that infants' attention was equally captured by congruent and incongruent grasps, the former due to familiarity (and the salience of a food-related item, Reid et al., 2009), and the latter due to novelty. The Nc model showed a more prominent Nc for the younger infants, which accords with the fact that the Nc is not always elicited as infants approach the second post-natal year (e.g. Grossmann et al., 2007; alternatively Carver & Vaccaro, 2007).

The P400 was affected by the congruence of the grasp. There was a larger positive amplitude in the P400 window in response to the incongruent than the congruent grasp. A grasp-related P400 congruence effect has been reported previously (Bakker et al., 2015), as six-month-olds exhibited a larger P400 in response to actions in which a hand was directed toward an object rather than away from it.

Although this prior result suggests a larger P400 for congruent actions, a larger response to *incongruent* actions was found in the present study. This could be due to the testing of older infants in this study, as infants shift from preferences for familiar stimuli to novel ones with age (Wetherford & Cohen, 1973) and with experience (Hunter & Ames, 1988). If the action P400 reflects the mapping of experience – whether motor or visual – onto perceived actions, the results found here suggest that nine- to twelve-month-old infants distinguish between grasps on the basis of how they match a target object. From a "social relevance" perspective, incongruent grasps may signal a new means of using an object, which would be relevant for infants learning to grasp in different ways.

The effect of age on the P400, wherein the component is smaller overall at 11.5 compared to nine months, could reflect a variety of factors. including broader anatomical changes in early development, such as the closing of the fontanelles, which in turn affect the propagation of EEG signals (Noreika et al., 2020). It could reflect a change in processing away from social relevance and recognition processes in action perception, and towards higher-level semantic processing of action, such as those indexed by the N400. Similarly to the Nc, it could represent a developmental shift in ERP morphology. Indeed, the N290-P400 complex is known to change with development into the adult N170 (de Haan et al., 2003), so it is not surprising that the P400 would attenuate with age. However, the interaction between age and congruence, such that nine-month-olds exhibited a less positive incongruent P400 response, would suggest that even if the P400 overall is attenuating with age, the distinction between the stimuli is stronger for the older infants. This is borne out by Figure 3.

The N400 was also affected by stimulus congruence. A larger (more negative) N400 is typically associated with incongruent stimuli (Kutas & Federmeier, 2011), but here we found a larger N400 for congruent stimuli. Other studies have reported the presence of an N400 in nine-month-old infants (Reid et al., 2009; Kaduk et al., 2016). This typically manifests as a negative *deflection* in the waveform in response to the incongruent but not the congruent stimulus. Figures in Reid and colleagues (2009) show an overall more negative waveform in response to the congruent action, but with no further negative deflection in the N400 window. In contrast, the results presented here show a negative-going peak in both conditions.

The conflict between N400 result of the present study and other developmental studies may be due to multiple issues. The first is that the N400 component overlapped with the long tail of the P400 component, meaning that the large positive P400 component for the incongruent stimulus pulled the measured N400 amplitude upward, creating an apparent difference in peak amplitude by condition where perhaps none existed. The second may be that the developmental trajectory of the action N400 differs from that of the linguistic N400 (as suggested by Junge et al., 2021). Congruent stimuli may elicit a larger N400 response as the infant first learns to generate and access action predictions that are based on the meaning, or semantics, of objects and gestures, rather than on familiarity or recognition. This explanation is not completely satisfactory, as in other studies nine-month-olds have not shown any N400 peak in response to congruent or expected actions, only to incongruent actions (Kaduk et al., 2016; Reid et al., 2009).

Behavioural studies have shown that infants with more advanced grasping ability are better at distinguishing between congruent and incongruent grasps (Daum et al., 2011; Loucks & Sommerville, 2012). Bakker and colleagues (2015; Bakker,

Sommerville & Gredebäck, 2016) also found that power grasping experience mediated the effect of grasping congruence on an action-related ERP, specifically the P400. This suggests that the neural encoding of grasping actions is affected by infants' motor experience of grasping. In the case of precision grasping, we did not find any unequivocal links between infants' precision grasping performance in the laboratory setting, and their ERPs in response to others' congruent and incongruent grasps on objects. Descriptively, infants who can perform a precision grip show a larger P400 response to others' incongruent grips, particularly at nine months of age. This trend, while in accordance with prior work, does not reach the threshold for significance.

For the N400, there was a difference in amplitude by age and by the production of precision grasping. Specifically, at nine months, precision graspers showed a more positive N400 component than non-precision graspers, whereas at 11.5 months, this effect was reversed. With no attendant effect of congruence, it is difficult to account for this difference except as a potential maturational change, with the typical negative N400 morphology seen most clearly in older infants with precision grasping ability.

There are a number of limitations with the present study. In the same experimental paradigm, adults did not show any effect of the actor's grasp type, nor of the grasp type by congruence interaction on N400 amplitude (Ní Choisdealbha, 2016), but this does not mean that infants would not encode the congruence of whole hand and precision grasps differently. Indeed, Bakker and colleagues (2015) did not find the same effects of congruence on the P400 when they used a precision grasp instead of a whole-hand grasp in their stimuli. Ideally, more trials would have been obtained per condition to maximise the available pool of data for a grasp-type-by-congruence analysis, or different samples would have been shown the whole-hand and precision grasp stimuli, as in Bakker and colleagues' (2015) work.

The results of this study indicate that by the end of the first postnatal year, as infants are becoming more proficient graspers and learning to use precision grasps, they encode the fit between a type of grasp and an object's form. The Nc component, which indexes infants' allocation of attention to salient stimuli, was elicited by stimuli regardless of congruence, but the P400 and N400 components distinguished between others' grasps on the basis of congruence. The P400 result suggests that infants encode grasps on the basis of their congruence with a target object, showing a larger response when mapping incongruent grasps – with which they have less experience - onto their own representations of action than when mapping congruent grasps. With no significant link found between grasping ability and congruence-related differences in P400 amplitude, it may be that visual experience plays a stronger role here rather than motor experience, though descriptive trends in the data and prior research suggest that motor experience's effects cannot be ruled out. Finally, the N400 effect suggests that infants distinguish between grasping actions on a semantic level, generating expectations about actions based on higher-order information (such a function or shape). The reversed N400 effect, with a more negative ERP in response to the congruent stimuli, signals that further investigation of the developmental trajectory of this component is warranted. Overall, the results indicate that by nine months, infants attend to and encode the relationship between a grasping hand and the object it is acting upon, which means that during action perception they attend to the process as well as the outcome of an action.

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Data Availability: Files related to data processing are available at this link alongside data and scripts used in analysis: https://osf.io/9xah3/

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Supplementary Materials for Neural representations of grasp congruence during the emergence of precision grasping

Additional methods information

Grasping production task measures

To allow for greater variation in score, while also using tasks that had been previously designed for the measurement of motor ability, we sourced items from a developmental scale that was institutionally available (the Bayley Scales of Infant Development, BSID-II; Bayley, 1993). The use of the BSID-II items was not intended to create a comprehensive BSID. Rather, the items that were age-appropriate and related to grasping were selected. This selection encompassed six items, across three different objects or object pairs (a small pellet, a rod, a pencil and paper). The experimenter presented each item to the infant one-by-one in the above-listed order. Once the infant engaged with the item by reaching for, touching, and/or grasping it, the item was retrieved by the experimenter and the next one was presented. Performance was recorded using a video camera and a coder scored infants from 0 to 6 in accordance with Table S1. Some items are mutually exclusive. For example, an infant cannot perform items 41, 49, and 56 simultaneously, as they are all different types of grasp on a single object. Therefore, if they use the most advanced grasp (item 56), they get credit for items 41 and 49 as well (see OR statements in Table 1). This is in accordance with the instructions of BSID-II scoring. There was no stopping rule, all infants were presented with all items and non-engagement with the item was scored as 0.

The different items relate to different aspects of infants' grasping development, as described in the main manuscript's Introduction. Item 41 relates to

palmar or power grasping, the most fundamental form of voluntary grasping. It does not require thumb opposition. Item 49 then introduces thumb opposition, which Halverson (1931/1975) had noted as a key juncture in early grasping development, and which Butterworth et al. (1997) and Touwen (1975) distinguish from other power grips. Item 56 then refers to a precision grip. Item 57 captures thumb opposition, in this case on a different shape and size of item. Finally, items 58 and 59 capture grasping behaviours that align more with functional grasping (grasping an object for subsequent use) rather than pure motor execution.

Table S1: Bayley (BSID-II) motor development scale tasks used to measure grasping ability.

Item No.	Item description
41	Uses whole hand to grasp pellet OR performs items 49 or 56
49	Uses partial thumb opposition to grasp pellet OR performs item 56
56	Uses pads of fingertips to grasp pellet
57	Uses partial thumb opposition to grasp rod
58	Grasps pencil at farthest end OR performs item 59
59	Grasps pencil at middle

Across all infants who performed the grasping task, there was a mean score of 3.57 (SD = 1.62) out of 6, with nine-month-olds scoring 2.85 (1.59) and 11.5-month-olds scoring 4.38 (1.24). Scores out of six provide more granularity than a binary measure of whether the child could perform a precision grip or not. The Spearman

correlation between the full grasping score and the binary score was very high, $\rho(49) = 0.814$, p < 0.001 for all infants who took part in the production measure (n = 51).

Additional analysis information

Sensitivity analyses

Sensitivity analyses on multilevel data are complex so single level linear regressions were run for this purpose. These had the same factors and interactions as the multilevel models, but with participant identity included as a fixed rather than a random factor. Sensitivity analyses for multiple regression were then conducted in G*Power (Faul et al., 2011). For the Nc and P400 analyses, the required effect size (f²) was 0.01. The Nc model f² value was 0.035. For the P400 model, f² value was 0.052. For the N400 model, the critical f² was 0.017; the model value was 0.065. These effect sizes are relatively small, because the inclusion of each trial in the analysis creates additional unexplained variance (i.e. ERPs for the same condition varying over the course of the EEG recording). The thresholds are also small because of the large number of observations in the dataset.

These single-level models are not a perfect approach to the question of observed power in the actual models run for this study but are offered to the reader to make a holistic assessment of whether the results are sufficiently powered.

Results tables

Factor	Nc	P400	N400
Condition	F(1, 1761.74) = 0.511, p = 0.475	F(1, 1758.82) = 5.478, p = 0.019	F(1, 884) = 5.051, <i>p</i> = 0.025
Age	F(1, 37.28) = 2.689, p = 0.109	F(1, 37.06) = 2.053, <i>p</i> = 0.16	F(1, 884) = 0.308, p = 0.579
Hemisphere	F(1, 1730.61) = 5.044, p = 0.025	F(1, 1722.24) = 0.208, <i>p</i> = 0.649	
Precision grip execution	<i>F</i> (1, 37.06) = 3, <i>p</i> = 0.092	F(1, 37.06) = 0.024, <i>p</i> = 0.876	F(1, 884) = 1.45, p = 0.229
Condition * age	F(1, 1760.72) = 0.748, p = 0.387	F(1, 1752.82) = 4.472, p = 0.035	F(1, 884) = 2.237, <i>p</i> = 0.135
Condition * hemisphere	F(1, 1730.5) = 0.067, p = 0.796	F(1, 1722.48) = 0.198, <i>p</i> = 0.657	
Age * hemisphere	F(1, 1730.61) = 4.204, p = 0.04	F(1, 1722.24) = 0.769, <i>p</i> = 0.381	
Condition * precision	F(1, 1761.76) = 0.522, p = 0.47	F(1, 1758.82) = 1.583, <i>p</i> = 0.208	F(1, 884) = 0.334, <i>p</i> = 0.563
Age * precision	F(1, 37.25) = 0.018, p = 0.895	F(1, 37.06) = 0.749, <i>p</i> = 0.392	F(1, 884) = 3.998, <i>p</i> = 0.046
Condition * age * hemisphere	F(1, 1730.51) = 1.423, p = 0.233	F(1, 1722.48) = 0.699, p = 0.403	
Condition * age * precision		F(1, 1758.82) = 2.807, p = 0.094	F(1, 884) = 1.958, <i>p</i> = 0.162

Table S2: Tests of fixed effects, all analyses.

Table S3: Nc analysis, beta coefficients.

Effect	Beta estimate	Std. error	<i>p</i> -value
Condition (congruent rel. incongruent)	-0.138	0.941	0.884
Age (9 rel. 11 months)	-2.392	0.944	0.012
Hemisphere (left rel. right)	-2.09	0.818	0.011
Precision	0.967	0.741	0.196
Congruent * 9 months	1.65	1.132	0.145
Congruent * left hemisphere	0.747	1.12	0.505
9 months * left hemisphere	2.592	1.14	0.023
Congruent * precision	-0.588	0.814	0.47
9 months * precision	0.112	0.843	0.895
Congruent * 9 months * left hemisphere	-1.907	1.599	0.233
Intercept	0.661	0.747	0.377

Table S4: P400 analysis, beta coefficients.

Effect	Beta estimate	Std. error	<i>p</i> -value
Condition (incongruent rel. congruent)	3.888	1.94	0.045
Age (9 rel. 11 months)	4.59	2.101	0.03
Hemisphere (right rel. left)	1.247	1.383	0.368
Precision	-0.677	1.687	0.689
Incongruent * 9 months	-6.818	2.67	0.011
Incongruent * right hemisphere	-0.566	2.023	0.78
Incongruent * precision	-0.617	2.094	0.768
9 months * right hemisphere	-2.477	2.028	0.222
9 months * precision	-0.811	2.413	0.738
Incongruent * 9 months * right hemisphere	2.418	2.892	0.403
Incongruent * 9 months * precision	4.951	2.96	0.094
Intercept	-1.556	1.497	0.301

Bold font used for p < 0.05, bold italic for p < 0.1.

 Table S5: N400 analysis, beta coefficients.

Effect	Beta estimate	Std. error	<i>p</i> -value
Condition (congruent rel. incongruent)	-3.718	1.465	0.011
Age (9 rel. 11 months)	-2.821	1.396	0.044
Precision	-1.802	1.353	0.184
Congruent * 9 months	3.763	1.971	0.057
Congruent * precision	2.57	1.849	0.165
9 months * precision	4.417	1.855	0.018
Congruent * 9 months * precision	-3.637	2.6	0.162
Intercept	1.924	1.077	0.075

Analyses using granular grasping score

The primary analyses in this paper use a binary variable, which is whether or not the infant executed a precision grip on a small pellet in the lab. This is because many related studies have used binary measures (e.g. Daum et al., 2011; Loucks & Sommerville, 2012). As highlighted in the manuscript, coding of infant grasping behaviour is often more granular and indeed some of the cited work has used more granular measures, for example Bakker and colleagues (2015) who gave infants a score from 0 to 6, with three points available for components of the grasping action itself (arm extension, grip, and ability to hold), and three points available based on parent-report of the child's everyday production. The aim behind using the Bayley Scales measures was to obtain a granular score which reflected infants' use of other grasping skills, such as thumb opposition and functional grasping. Equivalent statistical models to the main manuscript's models are presented below, using the Bayley-derived score of 0 to 6 in lieu of the binary measure. Model fits, relative to a random effects only model, are as follows: Nc, $\chi^2(10) = 16.798 p = 0.079$; P400, $\chi^2(11)$ = 25.924 p = 0.007; N400, $\chi^2(7)$ = 15.016, p = 0.036. Differences from the main manuscript results, which used a single measure of precision grip production (item 56 in Table S1), are detailed below. Tests of factors' and interactions' contribution to model fit are in Table S6.

Nc model: Results are similar. Hemisphere and the age by hemisphere interaction contribute significantly to the model. The overall effect of age is marginal in this model, but in the same direction – a generally more negative waveform for nine-month-olds than 11.5-month-olds. As in the precision grip model, the Nc shows a more negative amplitude over the left than right electrodes, with a positive estimate on the left hemisphere by nine-month age group (Table S7).

P400 model: As in the main manuscript's precision grip model, the condition by age interaction makes a significant contribution to model fit. In contrast, there is no longer a significant contribution of condition as a main factor, but the three-way interaction between condition, age, and grasping score makes a significant contribution (whereas the condition by age by precision grip production interaction only made a marginal contribution to model fit in the main model). As in the precision grip model, the P400 amplitude is greater for the incongruent than the congruent stimulus, and for the nine-month than the 11.5-month age group, with a negative estimate on the interaction between these factors indicating that the difference between conditions is greater at 11.5 months. In contrast to the main manuscript model, we find interactions with the Bayley score. The negative estimate on the incongruent condition by grasping score interaction indicates that babies with higher grasping scores actually showed a smaller P400 in response to the incongruent stimulus. However, the threeway interaction between these variables and the nine-month age group shows that among the younger age group, those with higher grasping scores have larger P400 responses to the incongruent stimuli (Table S8).

N400 model: There are a few differences from the main manuscript model in terms of contributions to model fit. Condition now only makes a marginal contribution (p = 0.097). Instead of a significant contribution of age by grasping production, there are interactions between condition and age, and condition, age, and the granular grasping score. Model estimates, in line with the main manuscript model, show a significant effect of congruence (greater N400 response to the congruent stimulus), age (more negative amplitude at nine months), and age by grasping score (less negative N400 amplitude for more proficient graspers). The marginal effect of age by congruence in the main manuscript model is significant in this case, signalling that the

N400 to the congruent stimulus is less negative at nine months than 11.5 months. In addition, we find a three-way interaction between the congruent condition, the nine-month age group, and the Bayley score, indicating a more negative N400 to the congruent stimulus among more proficient graspers at nine months. Given that the morphologies of the 11.5-month-olds' ERPs suggest a difference in N400 response to the two conditions wherein the response to the incongruent stimulus is greater, this result may suggest that the more motorically proficient nine-month-olds are showing a more mature N400 morphology.

These analyses should be taken as secondary, exploratory analyses. They highlight that differences in encoding of action by infants with different levels of motor skill may be better captured (or, perhaps, exaggerated) by more granular measures of motor skill, relative to binary measures,

Factor	Nc	P400	N400
Condition	F(1, 1761.66) = 0.03, p = 0.862	F(1, 1747.37) = 1.673, p = 0.196	F(1, 862.24) = 2.789, p = 0.097
Age	F(1, 49.07) = 0.403, p = 0.528	F(1, 44.42) = 0.089, <i>p</i> = 0.767	F(1, 40.8) = 0.203, p = 0.655
Hemisphere	F(1, 1729.99.61) = 5.038, p = 0.025	F(1, 1723.55) = 0.213, p = 0.645	
Bayley grasping score	F(1, 44.51) = 0.87, p = 0.356	F(1, 42.83) = 0.004, <i>p</i> = 0.948	F(1, 36.99) = 1.566, p = 0.219
Condition * age	F(1, 1760.32) = 0.818, p = 0.366	F(1, 1747.37) = 11.913, <i>p</i> = 0.001	F(1, 862.24) = 6.216, p = 0.013
Condition * hemisphere	F(1, 1729.85) = 0.067, p = 0.796	F(1, 1723.76) = 0.2, <i>p</i> = 0.655	
Age * hemisphere	F(1, 1729.99) = 4.204, p = 0.04	F(1, 1723.55) = 0.775, p = 0.379	
Condition * Bayley grasping score	F(1, 1759.76) = 0.002, p = 0.965	F(1, 1756.66) = 0.009, p = 0.923	F(1, 869.71) = 0.631, p = 0.427
Age * Bayley grasping score	F(1, 44.97) = 0.041, <i>p</i> = 0.84	F(1, 42.83) = 0.817, <i>p</i> = 0.371	F(1, 36.99) = 0.891, p = 0.351
Condition * age * hemisphere	F(1, 1729.85) = 1.432, p = 0.232	F(1, 1723.76) = 0.7, <i>p</i> = 0.403	
Condition * age * Bayley grasping score		F(1, 1756.66) = 9.606, p = 0.002	F(1, 869.71) = 4.803, p = 0.029

 Table S6: Tests of fixed effects, all Bayley score analyses.

 Table S7: Nc Bayley score analysis, beta coefficients.

Effect	Beta estimate	Std. error	<i>p</i> -value
Condition (congruent rel. incongruent)	-0.568	1.485	0.702
Age (9 rel. 11 months)	-2.533	1.511	0.098
Hemisphere (left rel. right)	-2.094	0.818	0.011
Bayley grasping score	0.109	0.296	0.714
Congruent * 9 months	1.744	1.18	0.14
Congruent * left hemisphere	0.75	1.12	0.503
9 months * left hemisphere	2.599	1.14	0.023
Congruent * Bayley grasping score	0.012	0.288	0.966
9 months * Bayley grasping score	0.064	0.316	0.841
Congruent * 9 months * left hemisphere	-1.913	1.599	0.232
Intercept	0.795	0.561	0.576

	Table S8:	P400	Bayley	score and	alysis, k	oeta c	oefficients.
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Effect	Beta estimate	Std. error	<i>p</i> -value
Condition (incongruent rel. congruent)	11 0492	4 016	0.006
	11.0432	4.010	0.000
Age (9 rel. 11 months)	8.2123	3.762	0.031
Hemisphere (right rel. left)	1.25	1.25	0.366
Bayley grasping score	0.53	0.675	0.434
Incongruent * 9 months	-16.873	4.762	0.0004
Incongruent * right hemisphere	-0.563	2.02	0.78
Incongruent * Bayley grasping score	-1.733	0.861	0.044
9 months * right hemisphere	-2.479	2.025	0.221
9 months * Bayley grasping score	-1.053	0.872	0.23
Incongruent * 9 months * right hemisphere	2.415	2.887	0.403
Incongruent * 9 months * Bayley grasping score	3.361	1.085	0.002
Intercept	-4.288	3.119	0.172

	Table S9:	N400 Bayle	v score analysi	is. beta co	efficients.
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Effect	Beta estimate	Std. error	<i>p</i> -value
Condition (congruent rel. incongruent)	-8.316	3.439	0.016
Age (9 rel. 11 months)	-5.916	2.926	0.045
Bayley grasping score	-0.637	0.575	0.266
Congruent * 9 months	9.975	4.001	0.013
Congruent * Bayley grasping score	1.427	0.762	0.062
9 months * Bayley grasping score	1.513	0.697	0.032
Congruent * 9 months * Bayley grasping score	-2.094	0.956	0.029
Intercept	3.575	2.576	0.167

Pilot study with adults

Before collecting data from infants, a pilot study was run with an adult sample to find (1) whether an action N400 component was present in response to the stimulus image sequences, (2) whether the congruence of the presented grasp with the target object affected this component, and (3) whether the type of grasp (pincer versus power) had an effect. The N400 is seen in adults over parietal regions for language stimuli and over fronto-central regions for pictorial stimuli (Amoruso et al., 2013; Ganis, Kutas & Sereno, 1996), from about 300 or 400 milliseconds post-stimulus. It is generally of greater magnitude for semantically incongruous stimuli. In action research, a frontal N400 is found in response to actions in which an incorrect tool is used, for example if an iron is used to cut bread instead of a knife (Sitnikova et al., 2008) or if a screwdriver is used to open a lock (Bach et al., 2009). These findings informed the selection of the region and time window of interest in this adult pilot study.

Methods

Participants

Participants were recruited from the University's student population via an internal participant advertising system, or were invited to participate in the research following a query about obtaining EEG data for an arts project (n=5). No remuneration was offered but participants received credits towards their research skills modules where applicable. Ethical approval for all experiments reported in this report was granted by the University's research ethics committee.

Twenty-four participants were tested, and twenty-one (6 males) were included in the final sample. Three participants were excluded due to early termination of the session,

corrupted data and poor quality data, respectively. The age range of the included participants was 18 to 26 years (M = 20.7 years, SD = 2.65 years).

Procedure and stimuli

Participants' neural responses to the stimuli were collected using an EGI 128-sensor geodesic Hydrocel sensor net (Electrical Geodesics Inc., Oregon). Data were recorded via an EGI NA300 amplifier at 250Hz using EGI Netstation software, and re-referenced online to Cz. Stimuli were presented using Matlab (TheMathworks, Inc., Massachusetts) with Psychtoolbox (Kleiner, Brainard & Pelli, 2007). Participants viewed the stimuli on a 20-inch CRT monitor (refresh rate 60 Hz) at a visual angle of 23°, in a dark room. Within each sequence of three images, the first two images were displayed for 600ms and the third for 1s. Each image in the sequence followed the next with no interstitial. A white fixation cross appeared between sequences. The stimulus images were the same as those used in the infant study.

Participants were informed that they were part of a study to determine how different kinds of grasps are processed, in order to inform investigation of the same phenomenon in infants. They were given standard instruction to remain still and refrain from blinking during the stimulus display. Participants passively viewed 200 sequences and were offered breaks after each successive 50 trials. They could also request a break at any other time.

Analysis

Adult data were analysed using Netstation software. Data were bandpass filtered between 0.1 and 30Hz and segmented into 1200ms epochs extending from 200ms before the appearance of the third image in each sequence to 1s after. The Netstation default artefact detection process was applied to the data to reject segments with eye

movements or blinks. Channels that varied by more than 400µV within a segment were marked as bad, and segments with more than 15% bad channels were rejected. Channels that were marked as bad in more than 40% of segments were marked as bad throughout. The Netstation bad channel interpolation algorithm was then applied to the data. Baseline correction was applied to each segment based on the 200ms pre-stimulus period (in which the second of the images was onscreen) and data were then re-referenced to the average reference. Finally, an average ERP was computed per participant per condition.

The N200 and N400 responses were analysed in the adult dataset. The N200 is a potential adult analogue of the P400 (Gredebäck, Melinder & Daum, 2010). It was not considered as part of the original pilot study, which focused on the N400, but investigated after a later suggestion to check for effects analogous to the P400 . The Nc is not present in adult ERPs. Mean amplitude values were calculated for each participant over occipital channels in the 140ms to 240ms post-stimulus period (channels 58, 59, 64, 65, 68, 69, 89, 90, 91, 94, 95, 96) and over fronto-central channels in the 350 to 550ms post-stimulus period. The regions and time windows investigated are in accordance with previous N200 (Gredebäck, Melinder & Daum, 2010), pictorial N400 (Ganis, Kutas & Sereno, 1996) and action N400 (Amoruso et al., 2013) literature.

Results

Two 2-by-2 repeated measures ANOVAs were conducted on the data, one for each of the N200 and N400 windows. Within the N200 time window, there were no main effects – congruence, F(1,20) = 0.67, p = 0.42, $\eta^2 = 0.01$; grasp type, F(1,20) = 1.56,

p = 0.22, $\eta^2 = 0.03$. The interaction between congruence and grasp type was nonsignificant but marginal, F(1,20) = 3.99, p = 0.05, $\eta^2 = 0.06$.

Within the N400 time window, there was a main effect of grasp congruence (i.e. if the type of grasp used matched the form of the cup); F(1,20) = 9.369, p < 0.05, $\eta^2 = 0.08$. The mean amplitude of the response to the incongruent grasp was more negative than the mean amplitude of the response to the congruent grasp (Figure S1). There was no effect of grasp type (precision vs. power); F(1,20) = 0.033, p = 0.857, $\eta^2 = 0.001$) nor was there an interaction between the two factors; F(1,20) = 1.127, p = 0.3, $\eta^2 = 0.02$.



Figure S1: Mean amplitude over fronto-central electrodes (circled in the top-right electrode map) in adults in response to the critical grasp stimulus. Results indicate a larger N400 response to the incongruent than the congruent grasps, as evidenced in the 350-550ms epoch.

Discussion

Results show that adults process the interaction between hand and cup semantically, as evidenced by the presence of a fronto-central N400 which differed between grasps that were congruent or incongruent with the cup's shape. This response is modulated by the congruence of the performed grasp relative to the structure of the grasped cup. The lack of interaction between grasp congruence and type indicates that neither kind of grasp was more expected generally. This is important because of potential asymmetry in the frequency and flexibility of how these grasps are used – the more precise grasp on the round-edged cup is plausibly less incongruous than the whole-hand grasp over the handle of the handled cup. Regardless, results indicate that there was an N400 effect in the expected direction.

The results did not support the hypothesis that in adulthood the N200 encodes the congruence of an object-directed gesture in terms of the object's affordances. It may be that this component is sensitive only to the direction of the gesture relative to the object, as in previous work (Gredebäck, Melinder & Daum, 2010).

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