Developmental Psychology

Event-related potentials discriminate familiar and unusual goal outcomes in 5-month-olds and adults

--Manuscript Draft--

Manuscript Number:	DEV-2016-0539R1
Full Title:	Event-related potentials discriminate familiar and unusual goal outcomes in 5-month-olds and adults
Abstract:	Previous event-related potential (ERP) work has indicated that the neural processing of action sequences develops with age. While adults and 9-month-olds use a semantic processing system, perceiving actions activates attentional processes in 7-month-olds. However, presenting a sequence of action context, action execution and action conclusion could challenge infants' developing working memory capacities. A shortened stimulus presentation of a highly familiar action, presenting only the action conclusion of an eating action, may therefore enable semantic processing in even younger infants. The present study examined neural correlates of the processing of expected and unexpected action conclusions in adults and infants at 5 months of age. We analyzed ERP components reflecting semantic processing (N400), attentional processes (negative central in infants; P1, N2 in adults) and the infant positive slow wave (PSW), a marker of familiarity. In infants, the PSW was enhanced on left frontal channels in response to unexpected as compared to expected outcomes. We did not find differences between conditions in ERP waves reflecting semantic processing or overt attentional mechanisms. In adults, in addition to differences in attentional processes on the P1 and the N2, an N400 occurred only in response to the unexpected action outcome, suggesting semantic processing taking place even without a complete action sequence being present. Results indicate that infants are already sensitive to differences in action outcomes, although the underlying mechanism which is based on familiarity is relatively rudimentary when contrasted with adults. This finding points toward different cognitive mechanisms being involved in action processing during development.
Article Type:	Article
Keywords:	action perception; event-related potentials; semantic processing; social cognition; N400; PSW
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Dear Dr. Susan J. Hespos,

Dear Reviewers,

Thank you very much for your review of our manuscript “Event-related potentials discriminate familiar and unusual goal outcomes in 5-month-olds and adults”. The reviewers’ thoughtful comments were very helpful in revising the manuscript. We believe that the manuscript, especially the Introduction and the Discussion, has improved as a result of the reviews, and we thank you for considering our article for publication in Developmental Psychology. In the following, please find the Reviewer’s comments and questions in italic and our replies in non-italic letters. We have now added page numbers to the manuscript to facilitate the review process. The page numbers refer to the manuscript without track changes, although we also added a version of the manuscript including track changes.

GENERAL REMARKS

Introduction

When reappraising our introduction in light of the comments provided by the reviewers, we agree that the Introduction needed more clarity.

With regard to the many comments concerning the Introduction, we decided to completely rewrite the Introduction. We now state our main goal of the study more explicitly at the beginning of the Introduction: “The current study aims to shed light on the neural processes taking place during action perception in early infancy and in adulthood.” (page 3)

We also leave out the model proposed by Gredebäck and Daum (2015) and concentrate more clearly on the relevant literature on infants’ action understanding with regard to behavioral studies prior to moving on to the advantages of using ERPs to examine this issue. After describing the previous study by Reid et al. (2009), we present the rationale of the present study in more detail and also highlight more clearly why we examined 5-month-olds and why we assessed the N400, Nc and PSW in the infant sample.

We think that the Introduction now leads more directly to, and focusses more on, the investigated research question.

EDITOR'S COMMENT

In line with the concerns of two reviewers regarding the sample size, a revision would need to present a power analysis justifying the sample size both for the infants and adults.

With regard to the power analysis, we have made the assumption that this request is for a power analysis for the non-significant results in the infant group. We looked into the literature about procedures of post hoc power analyses. To the best of our knowledge and from what we found in the literature, post hoc power analyses do not provide additional information, as the post hoc calculated power only reflects the p-value and should not be used for the interpretation of nonsignificant results (Goodman & Berlin, 1994; Hoenig & Heisey, 2001). However, the final sample size of 15 infants is within the normal range for infant ERP studies (Stets, Stahl, & Reid, 2012) and is comparable to the sample size of the 7- ($n = 13$) and the 9- ($n = 14$) month-olds in the previous Developmental Psychology study by Reid et al. (2009) that we have based our study on. It is also in line with the average sample size of 14 infants in visual ERP studies, which was shown as part of the meta-analysis by Stets et al. (2012) examining all published infant ERP studies. We are therefore confident that our results make a valuable contribution to the field.

REVIEWER'S COMMENTS

Reviewer 1

Introduction:

In the introduction (page 3, second paragraph), the authors discuss findings that visual experience and motor experience influence action prediction (i.e., days being fed vs grasping ability) as if they are similar and support the same mechanisms. These should be clarified and differentiated, especially given later discussion. In the following paragraph, they seem to contrast these (i.e. "interestingly...infants that do not yet use spoons..."). This should not be particularly surprising given Hunnius & Bekkering (2010) and Gredeback and colleagues' findings discussed in previous paragraph.

The first paragraph on page 4 concerning the role of active experience does not seem directly related to the current research. It seems that the 7-month-olds in the previous research by Reid and colleagues likely had little experience with spoons and should not differ in that respect from the 5-month-olds in this experiment.

We thank the Reviewer for highlighting these points. We no longer concentrate on the role of infants' own motor experiences in the manuscript as this was not the main focus of our study and we did not manipulate or control for infants' own experience with the presented action.

In general, the motivation for why 5-month-olds were tested instead of 7-month-olds was not clear. At the top of page 6, the authors justify the age choice with regards to the initial emergence of action understanding, but this leaves them unable to address the difference between 5 and 7 month olds in current and previous research. (see last paragraph of page 19)

We now state our reason for testing 5-month-olds more clearly on page 6: "In order to investigate neural correlates of early action understanding, we tested 5-month-olds. As behavioral results show, infants around this age are able to anticipate and evaluate eating actions (Gredebäck & Melinder, 2010, 2011; Hunnius & Bekkering, 2010; Kochukhova & Gredebäck, 2010), we therefore chose to examine 5-month-olds as we were particularly interested in the early neural correlates of action understanding, asking the question - is semantic processing already functioning when infants have just started to understand other people's actions, or do other processes, like attention, develop before semantic processing?"

We agree with the Reviewer that further studies are needed to directly compare our results to older age groups. We now explicitly discuss this issue in the discussion (page 23): "Another possible explanation for the lack of an N400 effect is that infants need an action context and need to perceive how an action is executed to semantically process that action. To test this idea, one could test 5-month-olds with the three-step action sequence presentation present in Reid et al. (2009). Given that even 7-month-olds did not show signs of semantic processing in that paradigm, we would not expect N400 effects to occur. Another possibility for future research would be to examine 7- and 9- month-olds with our simplified paradigm. This way, the influence of the complexity of the stimulus presentation could be tested against the influence of embedding an action outcome into an action sequence. "

And on page 27: "Testing different age groups with the same paradigm in future studies, for example testing 7- and 9-month-olds with our simplified stimuli, will help to disentangle the influence of the complexity of the presentation and the influence of the action context."

Further, the notion that 5 months is the "earliest age at which goal processing is reported" is controversial (e.g., at 3 months with motor intervention; at younger ages with non-human actions, according to some).

We agree with the Reviewer and deleted this sentence from the manuscript.

The justification for examining the PSW in infants is not evident. Was this examined but not significant in previous research (e.g., Reid et al.)? Or was this rather a posthoc analysis based on inspection of the data? (this is not necessarily wrong but should be stated openly)

We now state more clearly why the PSW is one potential ERP component that may give insights into action understanding in infants, even though it was previously not examined in relation to action understanding (page 6-7): "Another plausible component to differentiate between conditions is the positive slow wave (PSW). Even though it has not previously been investigated in the context of action understanding in infants, it is related to memory updating processes of only partially encoded stimuli (Nelson, 1997; Riby & Doherty, 2009; Snyder, 2010; Snyder, Garza, Zolot, & Kresse, 2010; Webb, Long, & Nelson, 2005). An enhanced PSW for the unexpected condition would reflect the increased neural resources which are needed to encode this action outcome. This would conversely show that the expected action outcome is already more familiar to the infants. Differences on the PSW would inform us about infants' familiarity with the action outcomes."

Methods/Results:

In the methods section, it would be good to know whether any adults were excluded and the approximate ages and sex of the adults.

We did not exclude any adult participant. This is stated in the Method section (page 9) “All tested adults were included in the final analyses.” Unfortunately, the sex and the exact age of the adult participants were recorded on a computer that was destroyed prior to retrieval of the information, when one of the authors moved to a new institution. We therefore are not able to provide additional information other than that stated in the manuscript.

Were participants rewarded for their participation?

We added this information to the manuscript on page 9: “Infants were given a t-shirt and £10 was given to the parents to cover travel costs.” and on page 9: “All tested adults were included in the final analyses. Adult subjects received £7 to participate.”

Relatedly, how many trials were rejected due to infants' lack of attention for the full 1000ms?

We now give a more detailed overview of the rejected trials in the Methods section (page 12):

“Following review of the video recordings of infant behavior, all trials in which the infant did not pay attention to the stimuli for the full 1000 ms of stimulus presentation were rejected from further analysis. On average, this included 53 trials in the expected (range of 24 – 99 trials) and 50 (range of 20 – 101 trials) in the unexpected condition in the infant sample. No significant difference between the amount of trials rejected based on the video analysis in the expected and in the unexpected condition were found, $t(14) = 1.49$, $p = 0.159$. The majority of trials was rejected because infants did not attend to the trials at all (mean of 37 trials in the expected and mean of 35 trials in the unexpected condition). In contrast, it was only in the minority of the excluded trials that infants attended to the trials at some point but not during the whole 1000 ms (mean of 16 trials in the expected and mean of 15 trials in the unexpected condition). For both measures (amount of trials infants did not attend to the screen at all and amount of trials infants only paid attention to the stimulus at some point during the stimulus presentation), we did not find differences between both conditions, $t(14) = 1.49$, $p = 0.159$ and $t(14) = 0.54$, $p = 0.596$, respectively.”

Were channels ever dropped/excluded due to noise?

We did not exclude single channels due to noise. Rather, whenever the peak-to-peak amplitude in any channel exceeded a threshold of 200 µV in a 200 ms window, the whole trial was excluded (page 12).

What was the reason that the mouth was open in the unexpected photos? Is it possible this divided the participants' attention between the location of the food and the open mouth? Could these low-level differences explain the PSW difference in infants? If so, what would this imply?

We used the stimuli by Reid et al. (2009) to make our results as comparable as possible to their results. The mouth was open in both conditions to keep the stimuli as perceptually similar as possible between both conditions. We expected to find differences on the PSW for pictures that infants are less familiar with. We cannot rule out that any perceptual unfamiliarity with or interest in the open mouth may have affected the PSW, but would not have contributed to differential effects of this study's conditions.

However, this seems unlikely as infants at that age very often experience people with an open mouth, for example when these people talk to the infant.

The idea that the difference in the distance between the food and the mouth plays a role here is interesting. If this had influenced infants' attention, we would have seen differences in the Nc component between conditions reflecting attentional processes, which was not the case.

The N400 findings (starting on page 12) would be confusing to follow if I had not previously read some of Reid and colleagues' research describing the Hoorman procedure. This analysis description should be described at the beginning before discussion of number of time windows, etc. Similarly, when reporting the significant results in adults (page 16), a brief explanation would help the reader interpret the time X condition interaction.

We now describe the Hoorman procedure in more detail on page (13-14):

"In the 9-month-olds in Reid et al. (2009), the N400 component was present in the unexpected condition and absent in the expected condition. To detect such differences in the morphology between ERP waves, for example the presence of a component in one condition and the absence of a component in the other condition, an analysis, as described by Hoormann, Falkenstein, Schwarzenau, and Hohnsbein (1998), can be performed. To conduct this analysis, the values of the amplitude of the ERP wave are extracted at several time points for both conditions and compared in a repeated measures ANOVA with within-subject factors of time and condition. If ERP waves differ in their morphology, the interaction between the factors time and condition will reach significance."

We also added an explanation of the adult results on page 19: "A significant condition x time interaction would suggest that the ERP waves differ between conditions, for example that the N400 would be present in only one condition. The ANOVA revealed a significant condition x time interaction, $F(3.84, 99.93) = 3.06$, $p = 0.022$, $\eta_p^2 = 0.105$. This significant interaction between condition and time highlights that there are differences in the morphology between the ERP waves of the two conditions. As can be seen in Figure 5, the N400 was only present in the unexpected condition but not in the expected."

The choice of the channels, number of windows and the overall time window should be justified for each analysis.

Please find below an overview of the reasons why we chose specific time windows and channels as well as a certain number of time windows for the N400 analyses. All references are now also stated in the manuscript.

	Time window	channels	Number of time windows (N400)
N400 infants	Based on Reid et al. (2009)	Based on Reid et al. (2009)	“we included only 15 instead of 17 time windows to be able to appropriately estimate the parameters given our sample size” page 13-14
Nc	Based on Kaduk et al. (2016)	Fronto-central channels, e.g. Hoehl, Reid, Mooney, and Striano (2008) and visual inspection	
PSW	Relatively early onset of PSW in line with previous studies (Reid, Striano, Kaufman, & Johnson, 2004; Striano, Kopp, Grossmann, & Reid, 2006) and visual inspection.	„The channels were chosen with regard to visual inspection of the grad averages and the existing literature showing that the PSW is most prominent on fronto-temporal electrodes (de Haan & Nelson, 1999; Reid et al., 2004; Snyder, Webb, & Nelson, 2002)” page 16	
N400 adults	Based on Reid et al. (2009) and visual inspection	Fronto-central channels based on previous studies (Amoruso et al., 2013; Ganis, Kutas, & Sereno, 1996) showing that pictures of action stimuli elicit a more frontal distributed N400 and visual inspection	Based on visual inspection of the course of the N400
P1	Based on Hillyard and Anllo-Vento (1998).	Occipital channels (Hillyard & Anllo-Vento, 1998) and visual inspection	
N2	Based on Folstein and Van Petten (2008)	Frontocentral channels (Folstein & Van Petten, 2008) and visual inspection	

I found the description of the data normalisation (top of page 13) confusing and hard to follow. This could be clarified and embellished.

We now added equations on page 14 to better illustrate how normalization was done. We hope this facilitates understanding of the calculations we made. The same normalization procedure was used in (Domínguez-Martínez, Parise, Strandvall, & Reid, 2015; Kaduk et al., 2016) but it was not described in detail in these papers.

In following up on the infant Nc, the posthoc analysis indicated that there was a regional difference in the expected condition, but the authors did not state the source of this regional difference.

We now performed follow-up paired t-tests (page 16): "Follow-up paired t-tests revealed that amplitude over the left hemisphere in the expected condition was more negative than over the right hemisphere, $t(14) = -3.671$, $p = 0.003$."

Discussion:

The interpretation of the lack of Nc effect in 5-month-olds (relative to 7-month-olds) was not clear. The authors hint at the notion that the Nc involves overt attention, but why this would be expected at 7, but not 5, months is not embellished upon. They suggest that the PSW reflects familiarity and distinguish this from attention, but is intuitively difficult to consider how familiarisation would be detected without attention.

We thank the Reviewer for raising these points.

We now state more clearly that the result of the Nc was not expected and mention one possible explanation why 5-month-olds differ from 7-month-olds here (page 23): "The Nc component was observed in the morphology of the ERP waveform in both conditions. The mean amplitude of the Nc in both conditions differed significantly from baseline with $t(14) = -3.652$, $p = .003$ for the expected condition and $t(14) = -6.164$, $p < .001$ for the unexpected condition. However, there was no statistical difference in the mean amplitudes of the Nc between conditions. This is in contrast to the results found in 7- and 9-month-olds that showed an enhanced Nc component in response to the expected condition that was related to eating (Reid et al., 2009) and consequently in contrast to our hypothesis. One possible explanation for this lack of difference in the Nc component may be that the mere presence of food itself elicits allocation of attention in 5-month-olds, whereas 7-month-olds are already more sensitive to the action of actually eating food instead of the mere presence of food. "

Based on the null results of the Nc we cannot conclude that no attention was involved in processing the stimuli. In contrast, both conditions elicited an equally distinct Nc component, indicating an equal amount of attention allocation. We now discuss the Nc result in more detail on page 23-24: "As the Nc was equally distinct in both conditions, we cannot conclude that attentional mechanisms play no role in action understanding in young infants. However, our results show that attentional mechanisms did not discriminate between expected and unexpected goal outcomes. "

Writing clarity:

In the abstract, it was unclear why 5-month-olds were suddenly tested and why the PSW was assessed.

We now partly rewrote the abstract and tried to state more clearly why we tested 5-month-olds within the given word limit for the abstract: “However, presenting a sequence of action context, action execution and action conclusion could challenge infants’ developing working memory capacities. A shortened stimulus presentation of a highly familiar action, presenting only the action conclusion of an eating action, may therefore enable semantic processing in even younger infants. The present study examined neural correlates of the processing of expected and unexpected action conclusions in adults and infants at 5 months of age.”

In addition, we mention more explicitly why we examine the PSW in infants: “We analyzed ERP components reflecting semantic processing (N400), attentional processes (negative central in infants; P1, N2 in adults) and the infant positive slow wave (PSW), a marker of familiarity.”

In the introduction (page 2), the second to last sentence of the first paragraph did not seem to speak to the issue brought up in the previous sentence.

We have now completely rewritten the Introduction and hope that it is written in a more coherent manner.

Throughout the manuscript, checks for word order, word choice and correct use of propositions should be more thoroughly done (e.g., page 3, first sentence of paragraph 2); page 4, last sentence of first paragraph (on = of); page 7, last sentence of first paragraph (think precursor is meant to mean subsequent outcome); page 19, 3rd sentence ("enhanced PSW [relative to]..."); page 20, first paragraph ("no statistical[ly] difference", "acti[o]n outcomes"

The manuscript was read and corrected by two native speakers.

Throughout the introduction, cognitive processes and concepts are referred to as "these aspects" or "associated processes" without clarification as to the referent

We now name the processes that we refer to (semantic processing, attention, encoding)

On page 6, paragraph 2, the justification of the stimuli/context seems to be confused with the justification of the age. When referring to the Hunnius & Bekkering and Kochukhova & Gredeback findings, the stimuli difference is not highlighted but the age seems to be.

We thank the Reviewer for this comment and hope that all issues in the Introduction have been clarified.

Top of page 7, it is not immediately clear that this entire paragraph focuses on adult hypotheses and not infants

To clarify this issue, we have now added the sentence: “For the adult sample, we hypothesized the following” on page 7.

Reviewer 2:

General evaluation

Although the paper addresses an interesting question, I have several concerns about the study design and interpretation of the data. My main concern is that the study is not designed to be able to support the developmental story that the authors would like to present. Although the current study is similar to previous ERP work that investigated infants' perception of goal-directed actions at 7- and 9-months of age (e.g. Reid et al., 2009) there are several important differences in the study design that preclude generalisation between the two studies. For example, it is unclear whether 9-month-olds would actually show an enhanced N400 response to the unexpected action conclusions using the current stimuli without any action context being presented. Demonstrating this seems like a crucial first step to support any conclusions about the possible cognitive mechanisms involved in this task at different ages.

Due to the fact that all of the authors have moved to new institutions, we are unable to test another age group with the same EEG system. Consequently we are unable test another sample without introducing potential confounds to the study. We agree with the reviewer that testing 9-month-olds with our simplified stimuli would provide further informative insights into the development of action understanding. We now discuss this idea in the discussion on page 23: “Another possible explanation for the lack of an N400 effect is that infants need an action context and need to perceive how an action is executed to semantically process that action. To test this idea, one could test 5-month-olds with the three-step action sequence presentation present in Reid et al. (2009). Given that even 7-month-olds did not show signs of semantic processing in that paradigm, we would not expect N400 effects to occur. Another possibility for future research would be to examine 7- and 9- month-olds with our simplified paradigm. This way, the influence of the complexity of the stimulus presentation could be tested against the influence of embedding an action outcome into an action sequence.“

And on page 27: “Testing different age groups with the same paradigm in future studies, for example testing 7- and 9-month-olds with our simplified stimuli, will help to disentangle the influence of the complexity of the presentation and the influence of the action context.”

As the authors pointed out on page 6: the absence of the N400 component in the 5-month-olds could either be due to a lack of action understanding or to the absence of the action context. Without additional measures that would shed light on the infants' processing of the action outcomes in the absence of an action context, like looking patterns, looking times, or pupil dilation, it seems impossible to distinguish between these two possibilities based on the current study's results.

We agree with the Reviewer that additional behavioral measures would clarify our results. Our study was not designed to measure pupil dilation or looking times, though. For our ERP measure, it is necessary to present as many trials as possible in a short amount of time. We therefore presented our stimuli only for 1000ms, which is shorter than the presentation in studies measuring different behavioral measures like looking behavior in response to stimuli investigating feeding actions (Gredebäck & Melinder, 2010; Hunnius & Bekkering, 2010; Kochukhova & Gredebäck, 2010).

To check for looking time differences between conditions in our study, we now added some analyses on the looking behavior of the infants in the Methods section (page 12):

"Following review of the video recordings of infant behavior, all trials in which the infant did not pay attention to the stimuli for the full 1000 ms of stimulus presentation were rejected from further analysis. On average, this included 53 trials in the expected (range of 24 – 99 trials) and 50 (range of 20 – 101 trials) in the unexpected condition in the infant sample. No significant difference between the amount of trials rejected based on the video analysis in the expected and in the unexpected condition were found, $t(14) = 1.49$, $p = 0.159$. The majority of trials was rejected because infants did not attend to the trials at all (mean of 37 trials in the expected and mean of 35 trials in the unexpected condition). In contrast, it was only in the minority of the excluded trials that infants attended to the trials at some point but not during the whole 1000 ms (mean of 16 trials in the expected and mean of 15 trials in the unexpected condition). For both measures (amount of trials infants did not attend to the screen at all and amount of trials infants only paid attention to the stimulus at some point during the stimulus presentation), we did not find differences between both conditions, $t(14) = 1.49$, $p = 0.159$ and $t(14) = 0.54$, $p = 0.596$, respectively."

In addition, we now highlight the promising usage of behavioral and neurophysiological measures for future work on page 25: "It is assumed that the reduction in complexity of the stimuli in the present study when contrasted with those used in Reid et al. (2009) will help to facilitate infant processing of the difference between expected and unexpected actions. This has not been verified via any independent means, such as assessing overall looking time or gaze shift patterns. Combining neurophysiological and behavioral measures would allow us to depict the broader picture of processes taking place during action understanding. A simultaneous application of both measurements very often seems impractical as different measures have different requirements (e.g. different timing of stimuli for different measures, required number of trials). Nonetheless, using the same stimuli in paradigms with different methods may be a promising next step for future research (Hoehl, Wahl, & Pauen, 2014; Wahl et al., 2013). For instance, an increase in pupil dilation in response to the action outcomes presented with and without the action context would inform us about the role of the presented action context for infants action understanding (Gredebäck & Melinder, 2010). Such combined methods are currently under development and, despite added complexities, stand to yield a number of advances in infancy research (Domínguez-Martínez, Parise, Strandvall, & Reid, 2015; Wass, de Barbaro, & Clackson, 2015)."

Introduction

The introduction is not very coherently organised and this needs to be improved. For example, the authors start by talking about a model proposed by Gredeback and Daum, followed by a paragraph *discussing the effect of action experience on action prediction, after which they discuss further stages of Gredeback and Daum's model, without logical transitions between the different paragraphs. It also seems like several different research questions are proposed throughout the introduction section. E.g. on page 1: whether the capacity to dishabituate when detecting changes in goal-directed behaviour or action anticipation is supported by different cognitive factors at different ages, page 3: how familiar actions that the infant cannot yet perform are encoded, page 3: how infants detect and interpret goal-directed actions, page 5: whether 5-month-old infants show evidence of semantic processing when presented with simplified presentations of unexpected action outcomes. The rationale for, and the main goal of the current study should be presented more clearly.*

Page 1: It is unclear to me why the authors propose that the ability to dishabituate when detecting change in goal-directed behaviours or the ability to anticipate actions would be supported by different cognitive 'factors' at different points in development? This does not seem like a very parsimonious hypothesis, and the authors need to provide a clearer rationale for this suggestion. Are there previous studies that suggest different mechanisms might underlie these abilities at different ages? What would these different 'cognitive factors' be?

Page 1: the authors cannot claim that they are aiming to shed light on the developmental trajectory of action perception from infancy to adulthood by testing one group of 5-month-olds and one group of adults.

Page 1, bottom of the page: the relevance of the model by Gredeback and Daum is unclear. The authors need to more explicitly discuss this model in relation to the present study's aims or objectives because otherwise it is unclear how these sentences relate to the rest of the text.

Page 3: Again, the authors cannot claim that they can facilitate a better understanding of developmental trajectories by using the same paradigm in one age group of infants and a group of adults.

Page 3: Again, the authors should specify why they think it is conceivable that differences in overt behaviour throughout development are a consequence of entirely different underlying cognitive processes.

Page 5: it is unclear to me based on what information infants were expected to form an expectation that could be violated if there were no pictures that showed the action context? The studies that are cited in favour of the idea that the presentation of an action context is most likely unnecessary (Kochukhova and Gredeback, 2010; Hunnius and Bekkering, 2010) actually both included a significant amount of action context, e.g. infants observed the actor looking at a plate, after which the spoon was picked up to take a piece of food from the plate, which was then brought to the mouth, in the study by Kochukhova and Gredeback. Based on what information did the authors hypothesise that the presentation of the action context was unnecessary? And that infants would be able to process the action conclusion stimuli semantically for these simplified stimuli?

We thank the Reviewer for highlighting ways how to improve the manuscript. With regard to the Reviewer's comments, we have now completely rewritten the Introduction. We left out the model by

Gredebäck and Daum (2015) and focused more specifically on the relevant literature for our study. In addition, we have sharpened our research question on page 3: “The current study aims to shed light on the neural processes taking place during action perception in early infancy and in adulthood.“

Also, we no longer claim to completely track developmental changes in the neural processing of goal-related stimuli within our study. However, we think it is still reasonable to state that – when considering the results of the current study in addition to the results by Reid et al. (2009) – we gain informative insights in the cognitive mechanisms taking place during action perception in the first postnatal year of life (page 7):

“Considering the results of the current study in addition to the prior literature related to the Nc and the N400 in 7- and 9-month-old infants (Reid et al., 2009) will provide us with informative insights into cognitive mechanisms taking place during action perception in the first postnatal year of life.”

Furthermore, we now state more clearly why we think that our simplified stimuli may enable semantic processing (page 5-6): “An alternative explanation is that younger infants found the paradigm, comprising a sequence of three images, to be too complex for optimal processing. The presented three-step sequence of action context, action execution and action conclusion may challenge infants’ working memory capacity specifically at the younger age group (Ross-sheehy, Oakes, & Luck, 2003). This overload in information may inhibit semantic processing. It may therefore be possible that even infants younger than 9 months of age possess the ability to process action information in a semantic manner, but the rather complex paradigm may have been unsuitable to elicit evidence for this ability. In order to address this alternative explanation, the present study reduced the complexity of the stimulus presentation: instead of presenting the complete three-step sequence of context, execution and conclusion (as in Kaduk et al., 2016; Reid et al., 2009), we presented only the picture of the action conclusion to the infants. We assume that this simplified presentation facilitates the processing of the stimuli, as no other information (i.e., action context, action execution) need to be kept in mind to evaluate the end state of the action. This assumption is in line with studies showing that reducing the complexity of stimuli influences the neurophysiological processes taking place in ERP studies (Peykarjou, Pauen, & Hoehl, 2014, 2015).”

Page 6: I think there is mistake here. The P1 and N2 component are suggested to be a precursor to the infant Nc component, while I think the authors instead meant to say that the infant Nc component is a precursor to the adult P1 and N2 components? This paragraph needs to be re-written to explain more clearly which components will be investigated in the infant group and which components will be investigated in the adult group.

We thank the Reviewer for highlighting our mistake. We now corrected it on page 8:

“In the adult sample, we therefore analyzed differences between conditions on the P1 component (Vogel & Luck, 2000) which is associated with arousal and the N2 component, which is associated with processes of orientation of attention and is suggested to be a successor to the infant Nc component (Folstein & Van Petten, 2008; Rothenberger, Banaschewski, Siniatchkin, & Heinrich, 2007). “

In addition, in the new Introduction, we now separated more clearly hypotheses and ERP components for the infant sample from the hypotheses and ERP components for the adult sample.

Page 12: Nc analyses: I may be missing something here but it seems to me that the significant interaction between condition and region of interest suggests that there are differences in the difference between the Nc component for the expected and unexpected condition over the different areas. Therefore the analysis of the differences between the expected and unexpected condition over the different regions, which does not show any significant effects, seems to be the only correct follow-up test, and the authors' suggestion that the interaction was due to differences in the Nc amplitude between the different regions of interest only in the expected condition is not correct.

The significant interaction between region of interest and condition leaves the question open on whether the conditions differ on different regions of interest or if, within one condition, amplitudes of ERP waves differ between the regions. We agree with the Reviewer that the primary comparison is the difference between conditions. As stated, these comparisons did not reach significance. We therefore conclude that there are no differences between conditions on the Nc, and interpreted data in this way. However, to give the complete picture of the data, and as requested by Reviewer 1, it may be of interest to state the nature of the difference. We therefore included the additional analyses in the paper.

Page 14: It seems like even in the unexpected condition the slow wave was negative in amplitude and not positive? Can something be called a positive slow wave if the amplitudes of the waveform are not positive?

ERPs are typically regarded as relative deflections with regard to a baseline. The label “positive” slow wave may therefore be interpreted as a deflection into the positive direction, which can be seen in our data. The variation in infants’ ERPs is large. It is not unusual that infant ERP components are not always in location above or below the baselined X-axis that their names suggest (positive for the positive slow wave or negative for the Negative central or the N290). See Wahl, Michel, Pauen, and Hoehl (2013) for examples of an Nc component not being negative relative to baseline, Hoehl, Wahl, and Pauen (2014) for examples of the Positive Slow Wave not being positive relative to baseline and Halit, de Haan, and Johnson (2003) for examples of the N290 not being negative relative to baseline – though they all represent appropriately positive or negative deflections relative to surrounding activity.

Page 18: The authors need to elaborate on what they think the 'relatively rudimentary' cognitive systems are that the 5-month-old infants in the present study would have employed.

We now clarify this point in the manuscript on page 22: “But the mechanisms by which this is displayed indicate that the cognitive systems employed are relatively rudimentary, as they are based on familiarity and memory encoding processes.” And on page 24: “The result on the PSW analysis suggests that infants at 5 months of age process actions at the level of familiarity vs. novelty. It is therefore possible that differences in the PSW only occurred because infants were perceptually more familiar with food in the mouth than food at the head. It follows that this unfamiliarity elicited the enhanced PSW in the unexpected condition without awareness of what defines the novelty of this stimulus, that is, that the displayed action is unusual.”

Page 18: Considering that the participants in the current study were presented with many instances of both the expected and unexpected action outcomes it seems possible that infants may initially have shown an enhanced N400 in response to the unexpected action outcome but that after seeing the unexpected outcome stimuli repeatedly they would have stopped generating action predictions. Adults, who may have more established/robust expectations about eating actions, might have been less influenced by this. It would be informative if the authors could investigate the first half of the trials compared to the second half of the trials for those infants who provided a sufficient number of trials (> 20 in each condition).

We thank Reviewer 2 for this idea. There were 11 infants that provided more than 20 valid trials in each condition whom we included in the further analyses. We separately analyzed ERPs for the first and the second half of the trials of each subject.

N400: We performed the same Hoormann analyses as described for the full sample separately for the first and the second half of the trials. We found a significant interaction between condition and time in neither the first half (p = 0.547) nor the second half (p = 0.212).

As we think that this additional analysis is informative, we have included the result of the first half in the manuscript (page 15): "Infants' initial expectations about the presented eating action may have been overwritten by repeatedly seeing a person holding food to the head in the course of the experiment. To test for this idea, we performed the same analysis only for the first half of valid trials for infants that contributed more than 20 trials to each condition. This analysis included 11 infants. No significant condition x time interaction was found, p = 0.547."

And in the discussion page 22: "In our infant sample, no N400 component was produced for the unexpected condition when contrasted with the expected condition, even when we analyzed only the first half of trials to check for potential learning effects during the course of the experiment."

We further checked if enhanced familiarity with the unexpected outcome pictures influenced the results of the Nc and the PSW analyses.

Nc: We performed a 2x3x2 repeated measures ANOVA with within-subject factors condition (expected vs. unexpected), region of interest (left vs. vs. central vs. right) and half (first vs. second half of trials). We did not find a significant main effect of half or interaction with the factor half, all ps > .561. There was only a significant interaction between region of interest and condition, $F(2,10) = 5.506$, $p < .05$. As in the full sample, this interaction was due to differences between the regions of interest in the expected condition ($F(2,20) = 5.421$, $p < .013$, but not in the unexpected condition, $p = .450$. No differences between the expected and the unexpected conditions were found when comparing data only from the left, the central or the right region of interest, all ps > .376.

PSW: We performed a 2x2x2 repeated measures ANOVA with the within-subject factors condition (expected vs. unexpected), region of interest (left vs. right) and half (first vs. second half of trials). We did not find a significant main effect of half or interaction with the factor half, all ps > .149. There was only a significant interaction between region of interest and condition $F(1,10)=6.404$, $p = .03$. As in the full sample, this interaction seemed to be driven by differences between conditions only in the left hemisphere ($t(10) = 2.127$, $p = 0.059$) , but not by differences in the right hemisphere, $p = .504$.

The results of the separate analyses of the first and the second half of valid trials therefore resemble the results of all trials. This suggests that the lack of an N400 effect in the infant sample was not due to infants getting familiar with the unexpected outcome.

Page 18, bottom of the page: As the authors pointed out earlier in the manuscript, the absence of the N400 in the infants in the current study could also be due to the absence of the action context. This possibility needs to be acknowledged and discussed.

We agree with the Reviewer and now discuss the absence of the N400 effect in infants in more detail in the Discussion on page 23: “Despite simplification of the stimuli to facilitate processing, no N400 component was found. One explanation of this finding is, that 5-month-old infants do not utilize semantic systems when observing others’ action outcomes. Another possible explanation for the lack of an N400 effect is that infants need an action context and need to perceive how an action is executed to semantically process that action. To test this idea, one could test 5-month-olds with the three-step action sequence presentation present in Reid et al. (2009). Given that even 7-month-olds did not show signs of semantic processing in that paradigm, we would not expect N400 effects to occur. Another possibility for future research would be to examine 7- and 9- month-olds with our simplified paradigm. This way, the influence of the complexity of the stimulus presentation could be tested against the influence of embedding an action outcome into an action sequence.”

Page 20: the relevance of motor resonance to the current study is unclear to me. I think the authors should be a bit more explicit here.

We now leave motor resonance out of the discussion as it was not the main focus of our study and as we did not manipulate motor experience.

Page 20: it would be useful if the authors would provide some examples of those factors that they think are likely to prove fruitful in future research.

We now explicitly state that the combined usage of behavioral and neurophysiological measures may be fruitful in future research on page 25: “Combining neurophysiological and behavioral measures would allow us to depict the broader picture of processes taking place during action understanding. A simultaneous application of both measurements very often seems impractical as different measures have different requirements (e.g. timing of stimuli specific measures, number of trials). Nonetheless, using the same stimuli in paradigms with different methods may be a promising next step for future research (Hoehl et al., 2014; Wahl et al., 2013). For instance, an increase in pupil dilation in response to the action outcomes presented with and without the action context would inform us about the role of the presented action context for infants action understanding (Gredebäck & Melinder, 2010). Such combined methods are currently under development and, despite added complexities, stand to yield a number of advances in infancy research (Domínguez-Martínez et al., 2015; Wass, de Barbaro, & Clackson, 2015) “

Page 22: to claim that the results of behavioural studies on action perception may be driven by completely different cognitive mechanisms at different ages based on an ERP study with only two age groups, consisting of 5-month-olds and adults seems like too much of a stretch to me.

Given the fact that we cannot underpin this conclusion with our results within our study, we now deleted this statement in the manuscript. As stated above, we think it is worth considering our results in addition with the results by Reid et al. (2009) (page 7):

"Considering the results of the current study in addition to the prior literature related to the Nc and the N400 in 7- and 9-month-old infants (Reid et al., 2009) will provide us with informative insights into cognitive mechanisms taking place during action perception in the first postnatal year of life."

Relatedly, in the Discussion, we integrate our results in the findings of Reid et al. (2009) (page 27):

"As the paradigm in our study and the one used in Reid et al. (2009) differ in the substantial aspect of generating a complete context of an action including the execution of the context itself, direct comparisons of both studies are not valid except with the adult participants. However, when taking the differences in the paradigms into account, the results from the current study, when combined with the results by Reid et al. (2009), give us insight into the neural mechanisms underlying action perception in the first postnatal year of life and in adulthood. When presented with only an action conclusion, the infant brain at 5 months of age detects differences between expected and unexpected action outcomes. This is likely due to familiarity, as shown by differences in the PSW. At 7 months, action understanding is indexed via differences in attentional mechanisms, as evidenced by changes in the Nc (Reid et al., 2009) in the context of an action sequence. Finally, at 9 months of age, in addition to the enhanced attention to the salient eating stimulus, the N400 is present when a complete action sequence is presented. This indicates that semantic processing is involved in the processing of actions in a way that it continues into adulthood. For adults, even the presentation of the final action conclusion is sufficient for a semantic system to be activated in the detection of an unfamiliar action. The utilization of ERPs enabled us to disentangle the different underlying processes that drive action understanding at different points during development."

Page 23: again, the authors need to specify which 'relatively simple mechanism' they think the infants would have utilised in the present study.

We now explicitly name familiarity as the simple mechanism underlying infants' processing of our expected and unexpected goal outcomes on page 24: "This suggests that the unexpected action conclusion was most likely perceived as more novel and unfamiliar to the infants, whereas the expected outcome was already familiar and therefore elicited less prominent slow wave activity. The result of the PSW analysis suggests that infants at 5 months of age process actions at the level of familiarity vs. novelty. It is therefore possible that differences in the PSW only occurred because infants were perceptually more familiar with food in the mouth than food at the head. It follows that this unfamiliarity elicited the enhanced PSW in the unexpected condition without awareness of what defines the novelty of this stimulus, that is, that the displayed action is unusual."

Minor points

Page 3: ERPs are not agents and therefore it seems odd to suggest that 'they' have the capacity to inform on a topic, or the ability to assess a number of cognitive processes simultaneously.

We have rewritten the sentence on page 4:

"These studies leave the question open on *how* infants detect and interpret goal directed actions. This limitation can be overcome using neurophysiological measures like event-related potentials (ERPs). ERPs have a high temporal resolution and consist of well-defined components reflecting different steps during stimulus processing including semantic processing, allocation of attention, or memory updating."

Page 14: The figures of the grand average responses should be enlarged, as it is currently very difficult to discern the waveforms for the different conditions.

We have now enlarged the figures for the analyzed channels. Please find the grand averages for all channels for the infants, as well as the adults participants, as supplemental material. We hope the ERP waves of both conditions are now more clearly displayed.

Reviewer 3

This manuscript was clearly written, providing the reader with a review of relevant background. There were several aspects of this manuscript that could be strengthened, especially the inclusion of a 9-mo-old comparison group—which would enhance cross-study comparisons and the developmental conclusions proposed in the current study.

We agree with the Reviewer that testing a 9-month-old sample would be of great interest. As mentioned in response to other reviewers, we are not able to perform the study with another age group. However, we now explicitly mention this idea in the discussion on page 23: "To test this idea, one could test 5-month-olds with the three-step action sequence presentation present in Reid et al. (2009). Given that even 7-month-olds did not show signs of semantic processing in that paradigm, we would not expect N400 effects to occur. Another possibility for future research would be to examine 7- and 9-month-olds with our simplified paradigm. This way, the influence of the complexity of the stimulus presentation could be tested against the influence of embedding an action outcome into an action sequence."

And on page 27: "Testing different age groups with the same paradigm in future studies, for example testing 7- and 9-month-olds with our simplified stimuli, will help to disentangle the influence of the complexity of the presentation and the influence of the action context."

***Page numbers were not used in the document so comments are provided by section. ***

We now added page numbers to the manuscript to facilitate reviewing.

Introduction

"suggested to be a precursor to the infant Nc component" - the wording of this is inaccurate as the authors later refer to the Nc being a precursor to the adult N2 and P1 component (i.e., an adult measure cannot be a precursor to an infant measure)

We changed the sentence to "In the adult sample, we therefore analyzed differences between conditions on the P1 component (Vogel & Luck, 2000) which is associated with arousal and the N2 component, which is associated with processes of orientation of attention and is suggested to be a successor to the infant Nc component (Folstein & Van Petten, 2008; Rothenberger et al., 2007)." (page 8)

"how the cognitive processes are employed in goal perception change across the first year of life" - The current design of this study does not permit for the examination of this question. Only one time point is examined during infancy (5 months), and it is unknown whether older infants would exhibit a similar pattern of ERP activity without contextual information provided in the previous study that is cited repeatedly for cross-study comparisons. The authors consider the present task to be an easier task, but without out any overlapping data for older infants, which would replicate and extend the previous work; thus, these developmental conclusions are limited at best. The present study does permit for direct comparison for adults across the two studies, which is a strength.

We agree with the Reviewer and now no longer claim that we assessed changes in goal perception during the first year of life within the present study. However, we believe that our results – when seen in addition to the previous study by Reid et al. (2009) – can provide insights in the different cognitive mechanisms taking place during action perception in the first postnatal year of life (page 7):

"Considering the results of the current study in addition to the prior literature related to the Nc and the N400 in 7- and 9-month-old infants (Reid et al., 2009) will provide us with informative insights into cognitive mechanisms taking place during action perception in the first postnatal year of life."

We now discuss our results considering results from the prior study by Reid et al. (2009) (page 27):

"As the paradigm in our study and the one used in Reid et al. (2009) differ in the substantial aspect of generating a complete context of an action including the execution of the context itself, direct comparisons of both studies are not valid except with the adult participants. However, when taking the differences in the paradigms into account, the results from the current study, when combined with the results by Reid et al. (2009), give us insight into the neural mechanisms underlying action perception in the first postnatal year of life and in adulthood. (…)"

We now more explicitly highlight the advantage of being able to directly compare our results to the adult results of Reid et al. (2009) on page 7:

"To further investigate the role of the context of an action, we also tested an adult sample with the same paradigm. As we kept the stimuli and the timing of the action conclusion pictures identical to Reid et al. (2009), comparing our results to the adult results in Reid et al. (2009) allowed us to directly examine the influence of the presented action context and action execution on the neural processing of expected and unexpected action conclusions."

And page 26:

"As we kept the stimuli and the timing of the action conclusion picture identical to the study by Reid et al. (2009), adult results of both studies can be directly compared."

Method

There was not an equal distribution in participant sex in the final sample (73% male)—this is not addressed in the manuscript.

We did not have any expectations about how the sex of the infant shall influence the results. That is why we did not include sex as a factor to the analyses. We had to exclude 7 infants from the final analyses. The sex of one excluded participant was unfortunately not registered. From the other 6 infants, 2 were female and 4 were male. Thus it does not seem that there was a systematic attrition of girls.

We now include this information to the manuscript on page 8:

"The sex of the infant participants was not equally distributed, but as we did not have any expectations about how the sex of the participants would influence the results, we have no reason to believe that this unequal distribution impacts the validity of our study. Another 7 infants (2 female, 4 male, 1 unknown) were tested but had to be excluded from the final sample because they failed to reach the minimum 10 artifact-free trials per condition (n = 5), or because of technical failure (n = 2)."

Basic demographic information is missing regarding both the infant (e.g., parent education, age, race; any other exclusionary criteria than full term, e.g., birth weight) and adult (e.g., age, race handedness, sex) samples.

Infants sample: The age of the infants is stated in the Methods section (page 8). No other information (e.g. parent education or race) were recorded for the infants as these were issues that were not considered to be relevant to this study. As such, it would have been unethical to capture this information as part of this study.

Adults sample: Unfortunately, the sex and the exact age of the adult participants were recorded on a computer that was destroyed prior to retrieval of the information, when one of the authors moved to a new institution. We therefore are not able to provide additional information other than the information stated in the manuscript.

The number of trials contributed per condition does not belong in the participants section, but later in the method section (e.g., procedure or EEG)

We shifted this information to the end of the EEG Recordings and Analyses paragraph on page 13.

Please explicitly state whether infants saw all 8 images (i.e., two images per tool/condition)—further were they any differences in behavior/EEG for the stimulus as a function of sex prior to collapsing across these images?

We now explicitly state on page 9: “Each infant saw each of the eight different stimuli.”

We did not expect any differences in behavior or neurophysiological response between the female and male stimuli. That is why we collapsed ERPs in response to the female and the male actor. Video coding revealed that infants equally attended to the male and the female stimuli: When comparing how many trials were coded as valid trials (infants attended the whole 1000ms of presentation to the stimulus), we found no difference between female and male actor: $t(14) = 1.55$, $p = 0.143$. To further test if infants react differently to the female or the male actor, we additionally compared the number of trials were infants looked at the stimulus at the onset of the presentation of the trial but looked away during the trial was presented (within the 1000ms). No differences were found between the female and the male actor: $t(14) = -0.31$, $p = 0.762$.

EEG Recording/Analysis - some information is missing (e.g., impedance level) that is requested as part of the Psychophysiology committee report for publication guidelines (Keil et al., 2014). Please review and include appropriate information.

We now added information about the impedance level on page 11-12: “For infants, the quality of the ongoing EEG data was inspected visually, and individual electrodes were examined if required, with the application of more paste should an electrode be too noisy or displaying channel offsets. For the adult sample, impedances were kept lower than 10 kΩ.”

We now included the range of valid trials for each condition for the infant and the adult sample (page 13) “On average each infant contributed a mean of 31 trials (SD = 12.95, range 15-54) to their average for the expected conclusion of the action condition and a mean of 32 trials (SD = 14.48, range 13-66) for the unexpected conclusion of the action condition. For the adult sample, analyses relied on a mean of 99 trials in the unexpected (SD = 25.99, 25-135) and 99 in the unexpected condition (SD = 25.09, range 28-136) with a minimum of 25 and 28 included trials, respectively.”

We also added which filter we used in EEGLAB (page 12). “Raw data were filtered offline with a 0.3 to 30 Hz bandpass filter using the pop_eegfiltnew function in EEGLAB”

Previous research reviewed in the introduction has indicated differences in looking time to expected and unexpected action outcomes. Please address where similar differences were found in the current paradigm (e.g., all trials that infants didn't pay attention to the stimuli for full 1000 ms were rejected).

The pictures in our study were only presented for 1000ms which is shorter than the stimulus presentation in looking time paradigms (Gredebäck & Melinder, 2010; Hunnius & Bekkering, 2010; Kochukhova & Gredebäck, 2010). To check for looking time differences between conditions in our study, we compared the amount of trials that were rejected because infants did not pay attention to the stimulus for the whole 1000ms between the expected and the unexpected condition. To examine in a more fine-grained manner whether infants reacted differently to the expected than to the unexpected condition, we compared the amount of trials in which infants looked at the stimulus during the onset of the picture but looked away while the picture was presented (within the 1000ms). This way, we would be able to detect differences in infants' behavior in response to the different conditions. We added these analyses to the method section (page 12):

"Following review of the video recordings of infant behavior, all trials in which the infant did not pay attention to the stimuli for the full 1000 ms of stimulus presentation were rejected from further analysis. On average, this included 53 trials in the expected (range of 24 – 99 trials) and 50 (range of 20 – 101 trials) in the unexpected condition in the infant sample. No significant difference between the amount of trials rejected based on the video analysis in the expected and in the unexpected condition were found, $t(14) = 1.49$, $p = 0.159$. The majority of trials was rejected because infants did not attend to the trials at all (mean of 37 trials in the expected and mean of 35 trials in the unexpected condition). In contrast, it was only in the minority of the excluded trials that infants attended to the trials at some point but not during the whole 1000 ms (mean of 16 trials in the expected and mean of 15 trials in the unexpected condition). For both measures (amount of trials infants did not attend to the screen at all and amount of trials infants only paid attention to the stimulus at some point during the stimulus presentation), we did not find differences between both conditions, $t(14) = 1.49$, $p = 0.159$ and $t(14) = 0.54$, $p = 0.596$, respectively."

Results

Adult - P1 - check electrode names for 01 (should be O1) and P10 (likely PO10)

We have now corrected these labels.

Discussion

First paragraph - the interpretation of the functional significance of all ERP components is include except the infant PSW, please state briefly here as well.

We have now included this information on page 22 "The PSW was enhanced for the unexpected condition relative to the expected condition on left frontal channels. As the PSW is related to memory updating processes for stimuli that are only partially encoded (Nelson, 1997; Riby & Doherty, 2009; Snyder, 2010; Snyder et al., 2010; Webb et al., 2005), the result suggests that enhanced activity was required to process the unexpected, thus unfamiliar action conclusions when contrasted with processing the expected, more familiar ones."

Cross-study comparisons must include the discussion of differences in the design (e.g., context) and limitations of corresponding "developmental" conclusions.

We now explicitly highlight that there are differences in the design between our study and the one by Reid et al. (2009) on page 27 “As the paradigm in our study and the one used in Reid et al. (2009) differ in the substantial aspect of generating a complete context of an action including the execution of the context itself, direct comparisons of both studies are not valid except with the adult participants. However, when taking the differences in the paradigms into account, the results from the current study, when combined with the results by Reid et al. (2009), give us insight into the neural mechanisms underlying action perception in the first postnatal year of life and in adulthood. When presented with only an action conclusion, the infant brain at 5 months of age detects differences between expected and unexpected action outcomes. This is likely due to familiarity, as shown by differences in the PSW. At 7 months, action understanding is indexed via differences in attentional mechanisms, as evidenced by changes in the Nc (Reid et al., 2009) in the context of an action sequence. Finally, at 9 months of age, in addition to the enhanced attention to the salient eating stimulus, the N400 is present when a complete action sequence is presented. This indicates that semantic processing is involved in the processing of actions in a way that it continues into adulthood. For adults, even the presentation of the final action conclusion is sufficient for a semantic system to be activated in the detection of an unfamiliar action. The utilization of ERPs enabled us to disentangle the different underlying processes that drive action understanding at different points during development. Testing different age groups with the same paradigm in future studies, for example testing 7- and 9-month-olds with our simplified stimuli, will help to disentangle the influence of the complexity of the presentation and the influence of the action context.”

And in the discussion of the N400 effect in infants (page 23): “Another possible explanation for the lack of an N400 effect is that infants need an action context and need to perceive how an action is executed to semantically process that action. To test this idea, one could test 5-month-olds with the three-step action sequence presentation present in Reid et al. (2009). Given that even 7-month-olds did not show signs of semantic processing in that paradigm, we would not expect N400 effects to occur. Another possibility for future research would be to examine 7- and 9- month-olds with our simplified paradigm. This way, the influence of the complexity of the stimulus presentation could be tested against the influence of embedding an action outcome into an action sequence.“

ADDITIONAL CHANGES

Due to an error with conveying numbers from tables to the manuscript, we have corrected the statistical values for the infant N400 analysis. The overall results remained the same.

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Event-related potentials discriminate familiar and unusual goal outcomes in 5-month-olds and adults

Running Head: Neural correlates of unexpected goal perception

Revision submitted: 27th of February 201

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Abstract

Previous event-related potential (ERP) work has indicated that the neural processing of action sequences develops with age. While adults and 9-month-olds use a semantic processing system, perceiving actions activates attentional processes in 7-month-olds. However, presenting a sequence of action context, action execution and action conclusion could challenge infants' developing working memory capacities. A shortened stimulus presentation of a highly familiar action, presenting only the action conclusion of an eating action, may therefore enable semantic processing in even younger infants. The present study examined neural correlates of the processing of expected and unexpected action conclusions in adults and infants at 5 months of age. We analyzed ERP components reflecting semantic processing (N400), attentional processes (negative central in infants; P1, N2 in adults) and the infant positive slow wave (PSW), a marker of familiarity.

In infants, the PSW was enhanced on left frontal channels in response to unexpected as compared to expected outcomes. We did not find differences between conditions in ERP waves reflecting semantic processing or overt attentional mechanisms. In adults, in addition to differences in attentional processes on the P1 and the N2, an N400 occurred only in response to the unexpected action outcome, suggesting semantic processing taking place even without a complete action sequence being present. Results indicate that infants are already sensitive to differences in action outcomes, although the underlying mechanism which is based on familiarity is relatively rudimentary when contrasted with adults. This finding points toward different cognitive mechanisms being involved in action processing during development.

Keywords: action perception, event-related potentials, semantic processing, social cognition, N400, PSW

Introduction

The ability to detect, process and interpret human actions is perhaps one of the most complex components of social cognition. It is therefore remarkable that the capacity to engage with observed actions and identify actions as goal directed in nature is present in infancy (see Gredebäck & Daum, 2015; Ní Choisdealbha & Reid, 2014 for an overview). A critical but mainly unaddressed issue remains; namely which processes, such as attentional or semantic processes, underlie action understanding at different ages. The current study aims to shed light on the neural processes taking place during action perception in early infancy and in adulthood. We examined neural correlates of the processing of expected and unexpected action conclusions in the context of food consumption, one of the first observed and experienced crucial actions in infancy.

Infants are remarkably good at understanding other people’s movements as goal directed actions (Gredebäck & Daum, 2015). Infants’ action understanding has mainly been studied using behavioral measures such as looking times, pupil dilation or anticipatory looking. Infants start to anticipate the goal of a grasping action between 6 and 12 months (Falck-Ytter, Gredeback, & von Hofsten, 2006; Kanakogi & Itakura, 2011) and this ability is related to their own grasping skills (Kanakogi & Itakura, 2011). Similar results were found for food consumption. At 6 months at the latest, infants anticipate that a cup or a spoon will be brought to the mouth (Hunnius & Bekkering, 2010; Kochukhova & Gredebäck, 2010). Not only do infants at 6 months of age have expectations about the end state of an action they observe, they are also able to evaluate whether an expected consequence occurred or not. This process has mostly been assessed with measures that reflect violation of expectation. In the context of grasping, infants as young as 6 months of age show longer looking times if an action consequence does not match with their expectations raised by the physical appearance of a grasp (Daum, Vuori, Prinz, & Aschersleben, 2009) or with their expectation about other people's goals (Woodward, 1998). With regard to feeding actions, starting at 4 months of age, infants seem to be more surprised when the bowl of a spoon is placed on the back of another person‘s hand (unexpected action outcome) than in the person's mouth (expected action outcome), as indicated by differences in pupil dilation (Gredebäck & Melinder, 2010, 2011). Thus, infants very early in life possess the ability to anticipate and evaluate other people's goal directed actions. The above mentioned studies used behavioral measures to investigate infants' action understanding. These studies leave the question open on *how* infants detect and interpret goal directed actions. This limitation can be overcome using neurophysiological measures like event-related potentials (ERPs). ERPs have a high temporal resolution and consist of well-defined components reflecting different steps during stimulus processing including semantic processing, allocation of attention, or memory updating. Critically, these processes may be active to a different degree at differing points in development (Reid et al., 2009).

With regard to action evaluation, the N400 event-related potential component has been related to semantic mismatch within adult populations when a perceived action violated expectations in a current context (see Amoruso et al., 2013 for an overview of the N400 in action contexts). An enhanced N400 was found in response to movie sequences of actions that included unexpected action outcomes in the context of eating (e. g. empty spoon put to mouth) as compared to expected outcomes (spoon conveying food put to mouth) (Reid & Striano, 2008). Another study presented images depicting the crucial stages of an action in sequence (Reid et al., 2009). Expectations about the action outcome were raised by 2 images of an ongoing action (image 1 action context: e. g. a person holding a pretzel; image 2 action execution: a person bringing the pretzel to the mouth) while a third image presented either an expected action conclusion (the pretzel in the mouth of the person) or an unexpected action conclusion (the pretzel at the ear of the person). In adults, an N400 component was elicited only in response to the unexpected outcome, reflecting a mismatch in the semantic processing of this action. The same effect was found in 9-month-olds indicating that infants at this age anticipate the outcome of an expected or unexpected action via the use of semantic processing systems. However, no N400 effect was found with infants at 7 months of age, although the negative central (Nc) component, related to attention mechanisms (Reynolds, 2015; Reynolds & Richards, 2005), differentiated conditions (Reid et al., 2009).

One explanation for this finding is that younger infants do not utilize semantic systems during action processing. Rather, discrimination between conditions is due to mechanisms related to attention, which according to Reid et al. (2009) was reflected in differences in the Nc component. As the Nc component is associated with allocation of attention (Reynolds, 2015; Reynolds & Richards, 2005) and is enhanced for familiar when compared to unfamiliar stimuli in infants (de Haan & Nelson, 1999), the highly familiar and evolutionarily significant event of eating elicited more activation on this component (Reid et al., 2009). An alternative explanation is that younger infants found the paradigm, comprising a sequence of three images, to be too complex for optimal processing. The presented three-step sequence of action context, action execution and action conclusion may challenge infants' working memory capacity specifically at the younger age group (Ross-sheehy, Oakes, & Luck, 2003). This overload in information may inhibit semantic processing. It may therefore be possible that even infants younger than 9 months of age possess the ability to process action information in a semantic manner, but the rather complex paradigm may have been unsuitable to elicit evidence for this ability. In order to address this alternative explanation, the present study reduced the complexity of the stimulus presentation: instead of presenting the complete three-step sequence of context, execution and conclusion (as in Kaduk et al., 2016; Reid et al., 2009), we presented only the picture of the action conclusion to the infants. We assume that this simplified presentation facilitates the processing of the stimuli, as no other information (i.e., action context, action execution) need to be kept in mind to evaluate the end state of the action. This assumption is in line with studies showing that reducing the complexity of stimuli influences the neurophysiological processes taking place in ERP studies (Peykarjou, Pauen, & Hoehl, 2014, 2015). From a practical standpoint, it was anticipated that these single-image stimuli would be more likely to be tolerated by young infants than multiple-image sequences, resulting in better data quality and more trials for inclusion in ERP averages. In order to investigate neural correlates of early action understanding, we tested 5-month-olds. As behavioral results show, infants around this age are able to anticipate and evaluate eating actions (Gredebäck & Melinder, 2010, 2011; Hunnius & Bekkering, 2010; Kochukhova & Gredebäck, 2010), we therefore chose to examine 5-month-olds as we were particularly interested in the early neural correlates of action understanding, asking the question - is semantic processing already functioning when infants have just started to understand other people’s actions, or do other processes, like attention, develop before semantic processing? Given that neural correlates of action perception have not been widely studied in a 5-month-old cohort, hypotheses for the infant sample included multiple possible neural correlates of action perception. If a less complex presentation of the action conclusion enables even younger infants to process the stimuli semantically, we hypothesized that an N400 would be found in response to the unexpected action conclusion. On the other hand, a lack of action understanding or the missing context may lead to no differences or to differences on a more basic processing level. This could be reflected in an enhanced Nc component for the expected condition indicating allocation of attention to the salient eating action (Reynolds, 2015; Reynolds & Richards, 2005) as it was the case in 7-, and 9-month-olds (Reid et al., 2009). Another plausible component to differentiate between conditions is the positive slow wave (PSW). Even though it has not previously been investigated in the context of action understanding in infants, it is related to memory updating processes of only partially encoded stimuli (Nelson, 1997; Riby & Doherty, 2009; Snyder, 2010; Snyder, Garza, Zolot, & Kresse, 2010; Webb, Long, & Nelson, 2005). An enhanced PSW for the unexpected condition would reflect the increased neural resources which are needed to encode this action outcome. This would conversely show that the expected action outcome is already more familiar to the infants. Differences on the PSW would inform us about infants' familiarity with the action outcomes. Any differences in these ERP components in response to the expected and unexpected action outcome stimuli could indicate whether the associated processes (N400: semantic processing, Nc: allocation of attention, PSW: familiarity) are functional during action processing at 5 months of age. Considering the results of the current study in addition to the prior literature related to the Nc and the N400 in 7- and 9-month-old infants (Reid et al., 2009) will provide us with informative insights into cognitive mechanisms taking place during action perception in the first postnatal year of life.

To further investigate the role of the context of an action, we also tested an adult sample with the same paradigm. As we kept the stimuli and the timing of the action conclusion pictures identical to Reid et al. (2009), comparing our results to the adult results in Reid et al. (2009) allowed us to directly examine the influence of the presented action context and action execution on the neural processing of expected and unexpected action conclusions. For the adult sample, we hypothesized the following - in line with Reid et al. (2009), we expected to find an N400 component in response to only the unexpected action conclusion in the adult sample (see also Mudrik, Lamy, & Deouell, 2010). As we presented photographic images of actions as stimuli, a frontal distribution of the N400 was expected (Amoruso et al., 2013; Ganis, Kutas, & Sereno, 1996). In the study by Reid et al. (2009), attentional mechanisms were involved in the processing of the stimuli in 7-, and 9-month-old infants as reflected in an Nc component of greater magnitude for the expected condition. This enhanced allocation of attention possibly indicated the high salience and evolutionary significance of the depicted eating action. In the adult sample, we therefore analyzed differences between conditions on the P1 component (Vogel & Luck, 2000) which is associated with arousal and the N2 component, which is associated with processes of orientation of attention and is suggested to be a successor to the infant Nc component (Folstein & Van Petten, 2008; Rothenberger, Banaschewski, Siniatchkin, & Heinrich, 2007).

Method

Participants

All subjects were recruited following a local media campaign for volunteers, from the area in and around Stockton-on-Tees, North East England. This study was conducted with the understanding and the written consent of each participant's caregiver or the participant in accordance with institutional protocols.

Infants

The final analysis was comprised of the data of 15 5-month-old infants (average age: 152 days, range: 147 – 167 days; 11 male, 4 female). The sex of the infant participants was not equally distributed, but as we did not have any expectations about how the sex of the participants would influence the results, we have no reason to believe that this unequal distribution impacts the validity of our study. Another 7 infants (2 female, 4 male, 1 unknown) were tested but had to be excluded from the final sample because they failed to reach the minimum 10 artifact-free trials per condition (n = 5), or because of technical failure (n = 2). All infants had to be born full term (37-42 weeks gestation). No other exclusionary criteria were applied. Infants were given a t-shirt and £10 was given to the parents to cover travel costs.

Adults

The adult sample consisted of 27 adults who were undergraduate students with normal or corrected to normal vision. All tested adults were included in the final analyses. Adult subjects received £7 to participate.

Stimuli

The stimuli were photographs depicting a male or a female actor, showing eating actions in two different ways: either with a spoon or holding the food. Those actions were presented either in an *expected* manner (food in mouth) or in an *unexpected* way (food touching other parts of the head). Figure 1 shows all stimulus pictures that were used in the study. Each infant saw each of the eight different stimuli. Stimuli were presented at full screen size (26 cm x 34 cm) on a 60 Hz 17-inch height adjustable stimulus monitor at a viewing distance of 90 cm. This produced a visual angle of 16.44° x 21.39°.

Figure 1: Stimulus material used in the study. Top line displays the expected action; bottom line displays the unexpected action both for the male and female actor. Note: images were displayed in color to participants.

Procedure

During recording, infants sat on their caregiver's lap in a dimly lit 2 x 2 metre testing area which was separated from the rest of the laboratory by black colored room dividers. A camera located above the center of the presenting screen recorded infants' looking behavior. If an infant became fussy or uninterested in the stimuli, the experimenter gave the infant a short break and attempted to resume the study when the infant was once again alert and calm. The testing session ended when the infant's attention could no longer be attracted to the screen. EEG was recorded continuously during the presentation.

The experiment consisted of a block of 32 action conclusion photographs with a division of male-female stimuli and expected-unexpected trials of exactly half each. The block could be repeated 9 times resulting in a maximum of 288 stimulus presentations. The two conditions were presented to the participant in a pseudo-randomized order with the constraint that the same condition was not presented more than three times consecutively.

Stimuli were presented utilizing the *Stim²-Gentask* computer software package by Neuroscan Compumedics (Charlotte, USA).

Each ERP time-locked image was presented on the screen for 1000 ms. Between the presentation of each image, the screen was white for a period of 700 ms only displaying a fixation cross in the center of the screen (see Figure 2 for an example of the stimulus presentation sequence). A 1700 ms period in between the onset of one critical stimulus and the next was used based on previous work with infants by Friedrich and Friederici (2011).

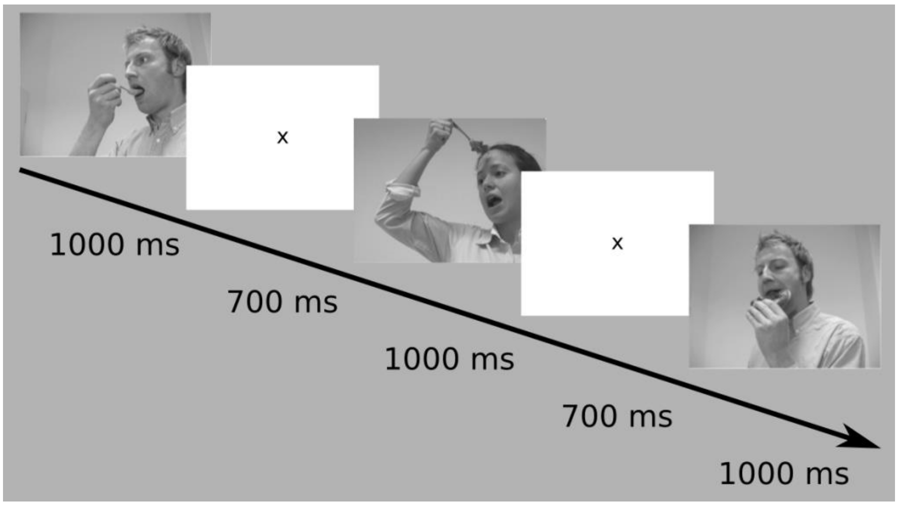

Figure 2: An example of the stimuli sequence presented to the participants: From top left to bottom right: expected-spoon *(1000 ms)*, inter-stimulus-interval *(700 ms)*, unexpected-spoon *(1000 ms)*, inter-stimulus-interval *(700 ms)*, expected-holding food.

EEG Recording and Analysis

EEG was recorded continuously from 32 scalp locations according to the 10-20 system, referenced online to AFz using Ag-AgCl ring electrodes with a sampling rate of 1Khz. For infants, the quality of the ongoing EEG data was inspected visually, and individual electrodes were examined if required, with the application of more paste should an electrode be too noisy or displaying channel offsets. For the adult sample, impedances were kept lower than 10 kΩ. Horizontal and vertical electro-oculograms (HEOG+ and VEOG+) were recorded bipolarly and the EEG data was amplified via a Neuroscan 32-channel amplifier. For additional data editing, the software EEGLAB version 13.4.4b was used (Delorme & Makeig, 2004). Raw data were filtered offline with a 0.3 to 30 Hz bandpass filter using the pop_eegfiltnew function in EEGLAB and re-referenced offline to the averaged mastoids (TP9, TP10). Data were segmented into epochs of waveform that comprised 200 ms prior to stimulus onset and 1000 ms following stimulus onset. Baseline was corrected using the 200 ms before stimulus onset. Following review of the video recordings of infant behavior, all trials in which the infant did not pay attention to the stimuli for the full 1000 ms of stimulus presentation were rejected from further analysis. On average, this included 53 trials in the expected (range of 24 – 99 trials) and 50 (range of 20 – 101 trials) in the unexpected condition in the infant sample. No significant difference between the amount of trials rejected based on the video analysis in the expected and in the unexpected condition were found, $t(14) = 1.49$, $p = 0.159$. The majority of trials was rejected because infants did not attend to the trials at all (mean of 37 trials in the expected and mean of 35 trials in the unexpected condition). In contrast, it was only in the minority of the excluded trials that infants attended to the trials at some point but not during the whole 1000 ms (mean of 16 trials in the expected and mean of 15 trials in the unexpected condition). For both measures (amount of trials infants did not attend to the screen at all and amount of trials infants only paid attention to the stimulus at some point during the stimulus presentation), we did not find differences between both conditions, $t(14) = 1.49$, $p = 0.159$ and $t(14) = 0.54$, $p = 0.596$, respectively. All remaining trials were scanned for artifacts using the automatic artifact detection implemented in ERPLAB version 5.0.0.0 (Lopez-Calderon & Luck, 2014). A trial was excluded from further analysis whenever the peak-to-peak amplitude in any channel exceeded a threshold of 200 µV in a 200 ms window. Window steps were set to 100 ms (Wahl, Michel, Pauen, &

Hoehl, 2013). The remaining segments were visually and manually edited for artifacts and blinks. Finally, data were averaged for the expected and the unexpected condition.

On average each infant contributed a mean of 31 trials (*SD* = 12.95, range 15-54) to their average for the expected conclusion of the action condition and a mean of 32 trials (*SD* = 14.48, range 13-66) for the unexpected conclusion of the action condition.

For the adult sample, analyses relied on a mean of 99 trials in the unexpected (*SD* = 25.99, 25-135) and 99 in the unexpected condition (*SD* = 25.09, range 28-136) with a minimum of 25 and 28 included trials, respectively.

Results

The level of significance was set to 0.05 if not stated otherwise and Greenhouse-Geisser correction was applied if applicable. Grand average of all channels for the infant sample can be found in Supplementary Material 1.

Infants

N400

Although an N400 analysis might have been pursued on the basis of previous work (Reid et al., 2009) and to establish whether the simplified stimuli would elicit such an effect in a younger age group, visual inspection did not show any evidence for an N400 (Figure 3). In the 9-month-olds in Reid et al. (2009), the N400 component was present in the unexpected condition and absent in the expected condition. To detect such differences in the morphology between ERP waves, for example the presence of a component in one condition and the absence of a component in the other condition, an analysis, as described by Hoormann, Falkenstein, Schwarzenau, and Hohnsbein (1998), can be performed. To conduct this analysis, the values of the amplitude of the ERP wave are extracted at several time points for both conditions and compared in a repeated measures ANOVA with within-subject factors of time and condition. If ERP waves differ in their morphology, the interaction between the factors time and condition will reach significance. To test for an N400 effect in our sample, we conducted the same analysis as with the infant participants in Reid et al.'s (2009) action observation study. However, we included only 15 instead of 17 time windows to be able to appropriately estimate the parameters given our sample size. Using the same time window (612 to 780 ms) and the same electrodes (P3, Pz, P4), a 2 x 15 repeated measures ANOVA with the within-subjects factors condition (expected vs. unexpected) and time (15 samples at one per 12 ms) was performed. As the signal of some participants may cross the x-axis in the selected time window, data were normalized for each participant and each condition using the following quotient to calculate the values for each time point

$$value\ at\ each\ time\ point = \frac{mean\ amplitude}{normalization}$$

with

$$mean\ amplitude = mean\ value\ of P3, Pz\ and\ P4\ for\ this\ time\ point$$

$$normalization = \frac{\sum normalized\ mean\ amplitudes\ of\ all\ time\ points}{number\ of\ time\ points}$$

$$normalized\ mean\ amplitude$$
$$= mean\ amplitude\ of\ each\ time\ point$$
$$- minimal\ amplitude\ of\ all\ time\ points\ of\ this\ participant\ and\ condition$$

A significant time x window interaction would indicate a difference in morphology. No condition x time interaction was found, $F(3.00, 42.01) = 1.47$, $p = 0.236$.

Infants' initial expectations about the presented eating action may have been overwritten by repeatedly seeing a person holding food to the head in the course of the experiment. To test for this idea, we performed the same analysis only for the first half of valid trials for infants that contributed more than 20 trials to each condition. This analysis included 11 infants. No significant condition x time interaction was found, $p = 0.547$.

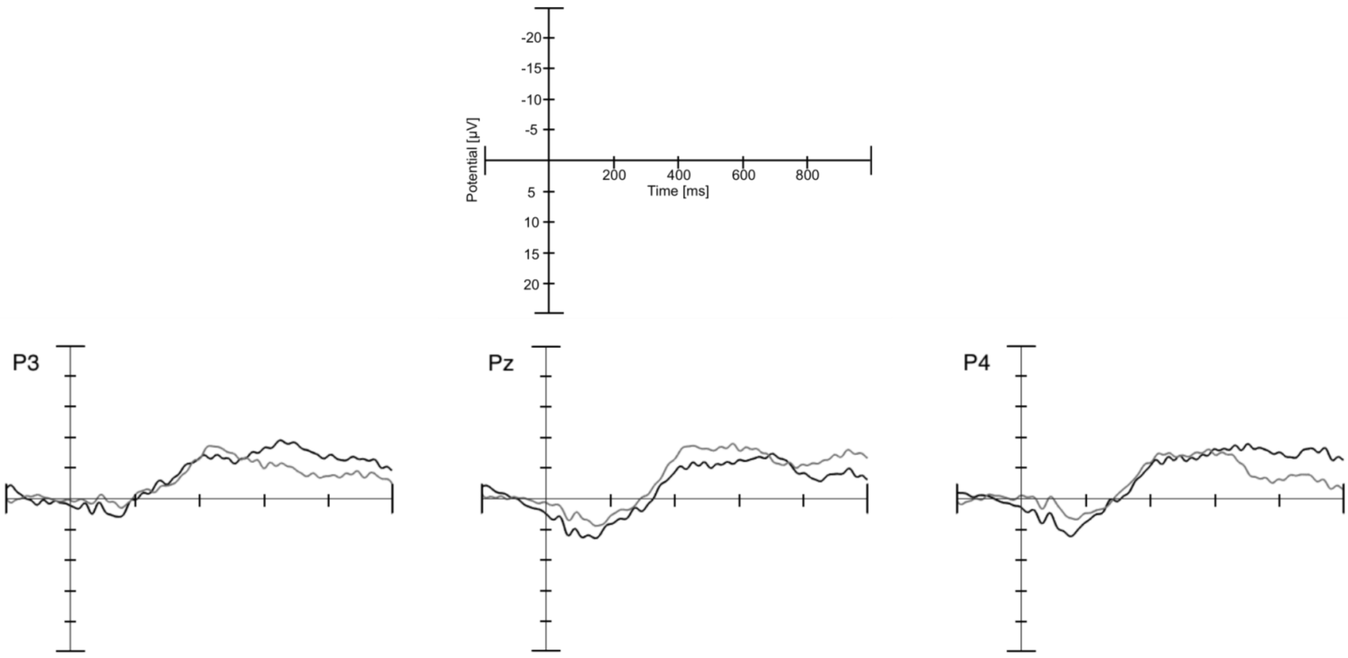

Figure 3: Channels analyzed for the N400 component in the infant sample. Black lines show the expected and grey lines refer to the unexpected condition. Note that negative is plotted up.

Nc

The mean amplitude for the Nc was assessed in left fronto-central (FP1, F3, FC5 and C3), fronto-central (Fz and Cz) and right fronto-central (FP2, F4, FC6 and C4) electrode clusters in a time window between 350 – 600 ms after stimulus onset, which fitted the resultant morphology and was congruent with other studies investigating this waveform (Hoehl, Reid, Mooney, & Striano, 2008; Kaduk et al., 2016). A 2 x 3 repeated measures

ANOVA was conducted with the within-subjects factors condition (expected vs. unexpected) and region of interest (left vs. central vs. right). This analysis revealed only a significant interaction between condition and region of interest, $F(1.39, 19.50) = 5.27$, $p = 0.024$, $\eta_p^2 = 0.273$, all other *p*s > 0.321. As post hoc repeated measures ANOVAs confirmed, this interaction was due to differences in the amplitude between the regions of interest only in the expected condition ($F(2,28) = 6.50$, $p = 0.005$, $\eta_p^2 = 0.317$). No such difference was found for the unexpected condition, $p = 0.879$. Level of significance for post hoc ANOVAs was set to $p < 0.025$. Follow-up paired t-tests revealed that amplitude over the left hemisphere in the expected condition was more negative than over the right hemisphere, $t(14) = -3.671$, $p = 0.003$. When comparing the expected and unexpected conditions separately for each region of interest with paired t-tests, no significant difference was found, all *p*s > 0.061. Level of significance for the post hoc paired t-tests was set to $p < 0.017$ for Bonferroni correction.

PSW

The 650 – 900 ms time window for the PSW analysis was selected due to the morphology of the data. Although this time window is shorter and earlier than the PSW window typically used in other studies (de Haan & Nelson, 1997; Webb et al., 2005), visual inspection of the data (see Figure 4) showed the slow wave tapering off before 1000 ms post-stimulus. Data were analyzed accordingly and in accordance with procedures used in other studies reporting earlier PSW effects (Reid, Striano, Kaufman, & Johnson, 2004; Striano, Kopp, Grossmann, & Reid, 2006) and hemisphere specific differences (Csibra, Tucker, & Johnson, 2001; Parise, Friederici, & Striano, 2010; Parise, Reid, Stets, & Striano, 2008; Reid et al., 2004). A 2 x 2 repeated measures ANOVA with within subject factors condition (expected vs. unexpected) and hemisphere (right vs. left) was conducted with the mean amplitude on left (FP1, F3, FC5, C3, CP5) and right (FP2, F4, FC6, C4, CP6) frontal channels in a time-window of 650 – 900 ms. Channels were chosen with regard to visual inspection of the grand averages and the existing literature showing that the PSW is most prominent on fronto-temporal electrodes (de Haan & Nelson, 1999; Reid et al., 2004; Snyder, Webb, & Nelson, 2002)

Results revealed no significant main effect of condition, $p = 0.134$, however a significant main effect of hemisphere was found, $F(1,14) = 8.10$, $p = 0.013$, $\eta_p^2 = 0.367$. The interaction between hemisphere and condition showed a significant effect, $F(1,14) = 6.13$, $p = 0.027$, $\eta_p^2 = 0.305$. Level of significance for post hoc tests comparing both conditions separately for the left and the right hemisphere was set to $p < 0.025$ for Bonferroni correction. Paired sample t-tests revealed that conditions differed significantly from each other only over the left hemisphere $t(14) = -2.56$, $p = 0.023$, $d = 0.660$, not over the right hemisphere, $t(14) = -0.211$, $p = 0.836$, $d = 0.055$. Over the left hemisphere, mean amplitude was more positive for the unexpected condition (mean = -6.36, SE = 2.05) as compared to the expected condition (mean = -10.92, SE = 2.20). No such difference was found over the right hemisphere (mean = -5.29, SE = 2.34 for the unexpected condition and mean = -5.66, SE = 2.34 for the expected).

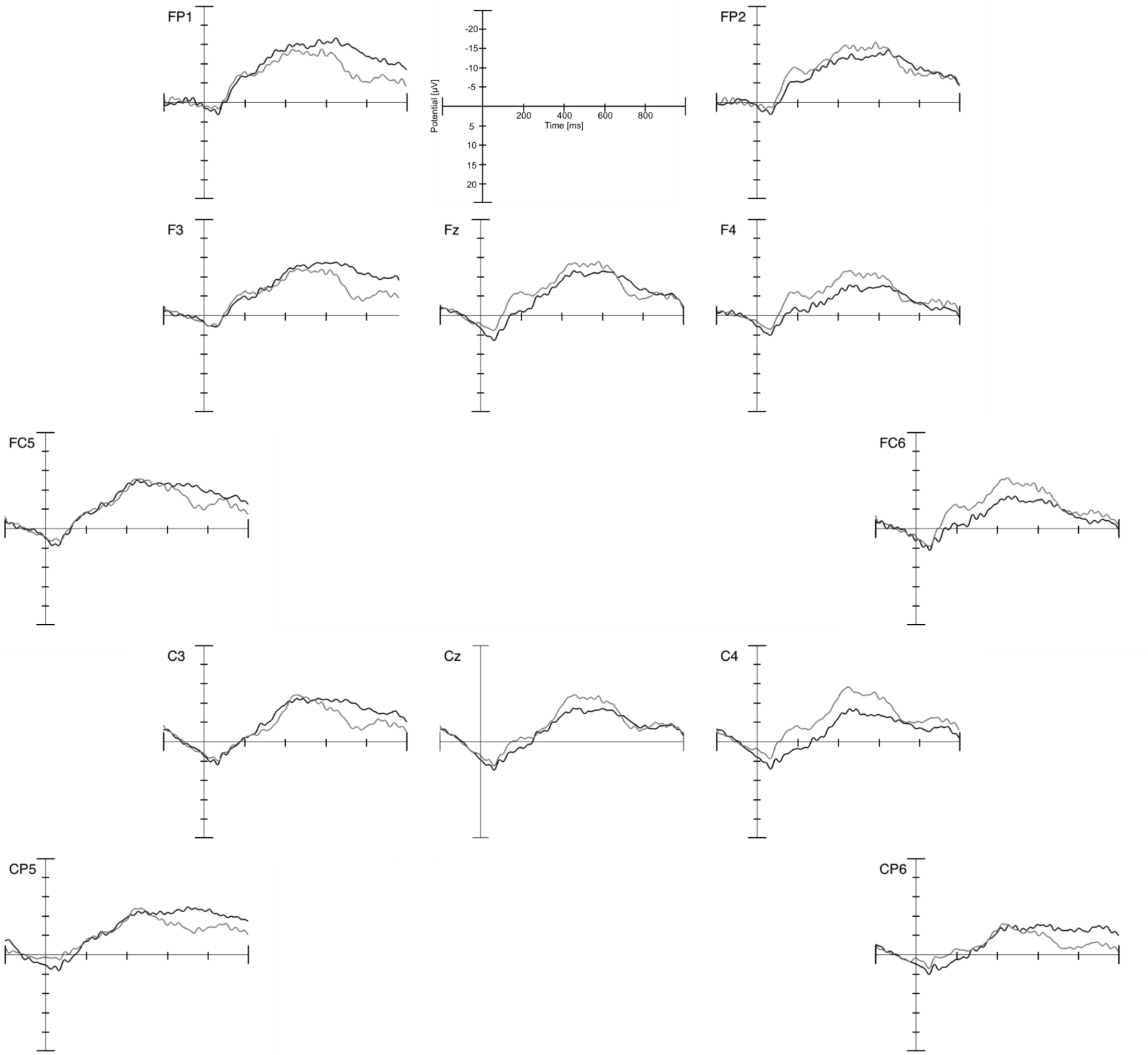

Figure 4: Channels analyzed for the Nc and PSW in the infant sample. Black lines show the expected and grey lines refer to the unexpected condition. Note that negative is plotted up.

Adults

The level of significance was set to 0.05 if not stated otherwise and Greenhouse-Geisser correction was applied if applicable. Grand average of all channels for the adult sample can be found in Supplementary Material 2.

N400

As in Reid et al. (2009) the N400 component was only visible in the unexpected condition, whereas no N400 was visible in the expected condition. To test EEG data for differences in morphology between conditions, Hoorman, Falkenstein, Schwarzenau, and Hohnsbein (1998) suggest a window analysis. Therefore we exported in total 13 amplitude values every 12 ms between 400 – 544 ms over fronto-central channels (FP1, FP2, F3, Fz, F4, F7, F8, FC5, FC6, C3, Cz, C4) where the N400 was most prominent. Again, as the signal of some participants may cross the x-axis in the selected time window, data were normalized for each participant and each condition using the same normalization quotient as for the infant data. A repeated measures ANOVA with the within-subject factors condition (expected vs. unexpected) and time (13 time points) was conducted. A significant condition x time interaction would suggest that the ERP waves differ between conditions, for example that the N400 would be present in only one condition. The ANOVA revealed a significant condition x time interaction, $F(3.84, 99.93) = 3.06$, $p = 0.022$, $\eta_p^2 = 0.105$. This significant interaction between condition and time highlights that there are differences in the morphology between the ERP waves of the two conditions. As can be seen in Figure 5, the N400 was only present in the unexpected condition but not in the expected. No main effects were found, all *p*s > 0.069.

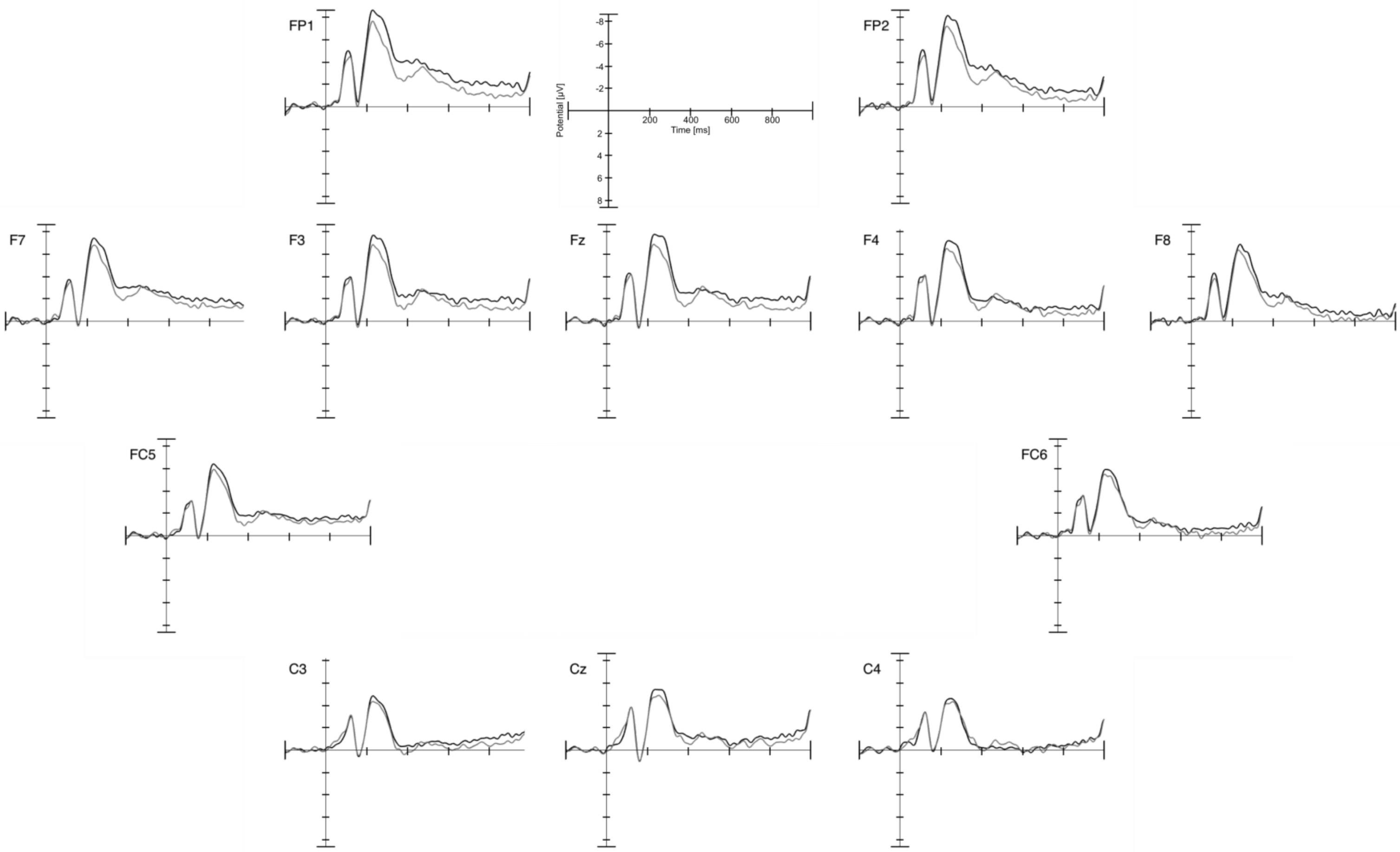

Figure 5: Channels analyzed for the N400 and the N2 component in the adults sample. Black lines show the expected and grey lines refer to the unexpected condition. Note that negative is plotted up.

P1

The visual component P1 is known to appear 80-130 ms after stimulus onset on occipital areas (Hillyard & Anllo-Vento, 1998). To investigate effects on the P1, mean amplitudes on left (O1 and PO9) and right (O2 and PO10) occipital channels in the time-window 80-130 ms served as the dependent variable. A 2 x 2 repeated measures ANOVA with the within-subject factors condition (expected vs. unexpected) and hemisphere (left vs. right) only yielded a significant main effect of condition, $F(1,26) = 5.83$, $p = 0.023$, $\eta_p^2 = 0.183$, with a more positive amplitude for the expected condition (mean = 3.71, SE = 0.44) than for the unexpected condition (mean = 3.27 SE = 0.40). No other main effect or interaction was found, all *p*s > 0.428.

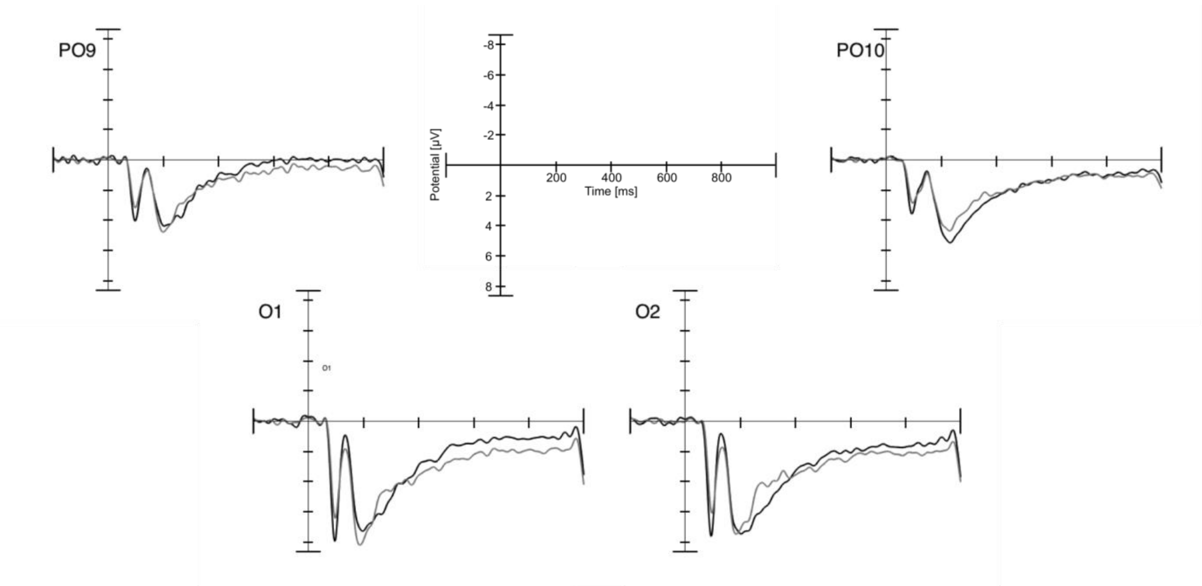

Figure 6: Channels analyzed for the P1 component in the adult sample. Black lines show the expected and grey lines refer to the unexpected condition. Note that negative is plotted up.

N2

The N2 component was analyzed on fronto-central left (FP1, F7, F3, FC5 and C3), fronto-central (Fz and Cz) and fronto-central right (FP2, F8, F4, FC6, C4) electrode clusters in the time-window 200-350 ms (Folstein & Van Petten, 2008). A 2 x 3 repeated measures ANOVA with the within-subject factors condition (expected vs. unexpected) and region of interest (left vs. central vs. right) only yielded a significant main effect of condition, $F(1,26) = 9.71$, $p = 0.004$, $\eta p2 = 0.272$, with a more negative mean amplitude for the expected (mean = -5.15, SE = 0.41) than for the unexpected condition (mean = -4.44, SE = 0.35). All other *p*s > 0.292.

Discussion

In this study, we examined the neural correlates that were associated with the perception of expected or unexpected action conclusions in early infancy and adulthood. In infants, the present experiment found that the PSW, but not the N400 or the Nc, differentiated expected and unexpected action outcomes at 5 months of age. The PSW was enhanced for the unexpected condition relative to the expected condition on left frontal channels. As the PSW is related to memory updating processes for stimuli that are only partially encoded (Nelson, 1997; Riby & Doherty, 2009; Snyder, 2010; Snyder et al., 2010; Webb et al., 2005), the result suggests that enhanced activity was required to process the unexpected, thus unfamiliar action conclusions when contrasted with processing the expected, more familiar ones. Infants are sensitive to differences in action outcomes in early development. But the mechanisms by which this is displayed indicate that the cognitive systems employed are relatively rudimentary, as they are based on familiarity and memory encoding processes. In adults, an enhanced N400 component occurred only in response to the unexpected action outcome, suggesting semantic processing of this action type even without the context of an action sequence being present. Results on the P1 and the N2 components indicate that attentional processes are active in adulthood similar to 7- and 9-month-old infants (Reid et al., 2009), at least when observing actions that are related to food consumption.

In our infant sample, no N400 component was produced for the unexpected condition when contrasted with the expected condition, even when we analyzed only the first half of trials to check for potential learning effects during the course of the experiment. There is currently some evidence that infants at 9 months of age use semantic systems to process actions (Kaduk et al., 2016; Reid et al., 2009), although no such studies have been conducted with infants as young as those investigated in the current study. In Reid et al. (2009), the complexity of the stimuli may have been one potential cause for a lack of N400 effect found in infants at 7 months of age. The present study attempted to simplify the stimuli yet aimed to still contain violations of expectation related to action outcomes in one condition but not the other. Despite simplification of the stimuli to facilitate processing, no N400 component was found. One explanation of this finding is, that 5-month-old infants do not utilize semantic systems when observing others' action outcomes. Another possible explanation for the lack of an N400 effect is that infants need an action context and need to perceive how an action is executed to semantically process that action. To test this idea, one could test 5-month-olds with the three-step action sequence presentation present in Reid et al. (2009). Given that even 7-month-olds did not show signs of semantic processing in that paradigm, we would not expect N400 effects to occur. Another possibility for future research would be to examine 7- and 9- month-olds with our simplified paradigm. This way, the influence of the complexity of the stimulus presentation could be tested against the influence of embedding an action outcome into an action sequence.

Despite the lack of an N400 effect, the ERP waveform showed other components of interest in relation to infant processing of actions. The Nc component was observed in the morphology of the ERP waveform in both conditions. The mean amplitude of the Nc in both conditions differed significantly from baseline with $t(14) = -3.652$, $p = .003$ for the expected condition and $t(14) = -6.164$, $p < .001$ for the unexpected condition. However, there was no statistical difference in the mean amplitudes of the Nc between conditions. This is in contrast to the results found in 7- and 9-month-olds that showed an enhanced Nc component in response to the expected condition that was related to eating (Reid et al., 2009) and consequently in contrast to our hypothesis. One possible explanation for this lack of difference in the Nc component may be that the mere presence of food itself elicits allocation of attention in 5-month-olds, whereas 7-month-olds are already more sensitive to the action of actually *eating* food instead of the mere presence of food. As the Nc was equally distinct in both conditions, we cannot conclude that attentional mechanisms play no role in action understanding in young infants. However, our results show that attentional mechanisms did not discriminate between expected and unexpected goal outcomes.

In the present work, the mean amplitude of the PSW differed between conditions over frontal channels of the left hemisphere. The fact that the PSW differed between conditions only over the left hemisphere aligns with studies that have previously reported left frontal ERP effects in infancy from 4 to 6 months of age (Csibra et al., 2001; Parise et al., 2010; Parise et al., 2008). The PSW has been related to familiarity detection, as it decreases with increased exposure to a stimulus (Snyder, 2010; Snyder et al., 2010) and when updating a memory representation of a partially encoded stimulus (Nelson, 1997; Webb et al., 2005). In the current study, the PSW was enhanced in response to the unexpected as compared to the expected condition. Thus, more activity was needed to encode the unexpected action outcome than the expected action outcome. This suggests that the unexpected action conclusion was most likely perceived as more novel and unfamiliar to the infants, whereas the expected outcome was already familiar and therefore elicited less prominent slow wave activity. The result on the PSW analysis suggests that infants at 5 months of age process actions at the level of familiarity vs. novelty. It is therefore possible that differences in the PSW only occurred because infants were perceptually more familiar with food in the mouth than food at the head. It follows that this unfamiliarity elicited the enhanced PSW in the unexpected condition without awareness of what defines the novelty of this stimulus, that is, that the displayed action is unusual.

The findings of the present study help to refine our knowledge of action understanding in early development and suggest that other processes precede semantic processing of action. These processes, as shown in the present study and in previous work (Reid et al., 2009), are likely to involve detection of familiarity and, later in development, allocation of attention to the presented stimuli. Further work is required to understand the earliest emergence of the semantic processing system and how its application to action processing corresponds to its application in language processing (Kaduk et al., 2016).

It is assumed that the reduction in complexity of the stimuli in the present study when contrasted with those used in Reid et al. (2009) will help to facilitate infant processing of the difference between expected and unexpected actions. This has not been verified via any independent means, such as assessing overall looking time or gaze shift patterns. Combining neurophysiological and behavioral measures would allow us to depict the broader picture of processes taking place during action understanding. A simultaneous application of both measurements very often seems impractical as different measures have different requirements (e.g. different timing of stimuli for different measures, required number of trials). Nonetheless, using the same stimuli in paradigms with different methods may be a promising next step for future research (Hoehl, Wahl, & Pauen, 2014; Wahl et al., 2013). For instance, an increase in pupil dilation in response to the action outcomes presented with and without the action context would inform us about the role of the presented action context for infants action understanding (Gredebäck & Melinder, 2010). Such combined methods are currently under development and, despite added complexities, stand to yield a number of advances in infancy research (Domínguez-Martínez, Parise, Strandvall, & Reid, 2015; Wass, de Barbaro, & Clackson, 2015).

In the present study, food stimuli were used because 5-month-old infants are familiar with feeding actions and observe their caregivers performing those actions multiple times daily. It is currently an open question whether other familiar but less motivationally salient object-directed actions, such as the phone- and hairbrush-related actions used in Hunnius and Bekkering (2010), elicit similar or distinct patterns of neural activity in infants of this age group. If the PSW effect in the present study was mainly driven by perceptual familiarity with the action, we would expect similar results to other actions which infants are familiar with.

As we kept the stimuli and the timing of the action conclusion picture identical to the study by Reid et al. (2009), adult results of both studies can be directly compared. In our adult sample, an N400 occurred only in response to the unexpected action outcome, reflecting the processing of a semantic mismatch for the familiar action condition. This result is in line with studies that found an enhanced N400 in response to unfamiliar or unexpected action outcomes using video stimuli (Reid & Striano, 2008; Sitnikova, Holcomb, Kiyonaga, & Kuperberg, 2008) or pictures (Mudrik et al., 2010). It replicates the results of Reid et al. (2009) and therefore suggests that no action context is needed for adults to process actions in a semantic way.

In addition to the effects on the N400, enhanced P1 and N2 amplitudes were found in response to the expected condition. As stimuli were controlled for luminance, we do not consider that these differences are due to psychophysical characteristics. However, an increased P1 is associated with higher arousal (Vogel & Luck, 2000). The N2 is associated with an orientation of visual attention in oddball paradigms (Folstein & Van Petten, 2008). The fact that both components are enhanced for the expected condition (related to eating) is in line with the infant results in Reid et al. (2009) showing an enhanced Nc component, indicating more allocation of attention, to the expected action. In accordance with the interpretation of Reid et al. (2009), an eating action is a highly salient event and of high evolutionary significance that may therefore lead to more arousal and attention than the unexpected condition. Interestingly, the similarities in the function and the assumed neural source of the N2 and the Nc led to the suggestion that the Nc may be a precursor in infants to the adult N2 (Rothenberger et al., 2007). This may explain the analogous results - the enhanced activity for the expected condition - in our adult sample and the infant sample in

Reid et al. (2009). However, see Marinović, Hoehl, and Pauen (2014) for a study that did not find corresponding results for infants and adults on the N2 in an oddball paradigm.

As the paradigm in our study and the one used in Reid et al. (2009) differ in the substantial aspect of generating a complete context of an action including the execution of the context itself, direct comparisons of both studies are not valid except with the adult participants. However, when taking the differences in the paradigms into account, the results from the current study, when combined with the results by Reid et al. (2009), give us insight into the neural mechanisms underlying action perception in the first postnatal year of life and in adulthood. When presented with only an action conclusion, the infant brain at 5 months of age detects differences between expected and unexpected action outcomes. This is likely due to familiarity, as shown by differences in the PSW. At 7 months, action understanding is indexed via differences in attentional mechanisms, as evidenced by changes in the Nc (Reid et al., 2009) in the context of an action sequence. Finally, at 9 months of age, in addition to the enhanced attention to the salient eating stimulus, the N400 is present when a complete action sequence is presented. This indicates that semantic processing is involved in the processing of actions in a way that it continues into adulthood. For adults, even the presentation of the final action conclusion is sufficient for a semantic system to be activated in the detection of an unfamiliar action. The utilization of ERPs enabled us to disentangle the different underlying processes that drive action understanding at different points during development. Testing different age groups with the same paradigm in future studies, for example testing 7- and 9-month-olds with our simplified stimuli, will help to disentangle the influence of the complexity of the presentation and the influence of the action context.

In conclusion, the results of this study demonstrate that infants at 5 months of age are capable of discriminating expected and unexpected actions, and that this is manifested at the level of neural activity. The finding that PSW was involved in this dissociation between conditions rather than other components which index higher levels of processing, such as attention or semantics, suggest that at 5 months of age infants utilize a relatively simple mechanism for detecting such differences based on familiarity. How this capacity relates to more complex forms of action processing, such as grasping the concept of affordance for tools as seen in later infancy, is yet to be understood. Adults however use a semantic system to make sense of actions even when an action sequence is missing.

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Event-related potentials discriminate familiar and unusual goal outcomes in 5-month-olds and adults

Running Head: Neural correlates of unexpected goal perception

~~Manuscript~~ Revision submitted:~~31st of august 2016~~ 27th of February 2017

Abstract

~~Previous event-related potential (ERP) work has indicated that infants at 9 months of age as well as adults process the outcome of an action via semantic processing systems, whereas this is not the case for 7-month-olds.~~ Previous event-related potential (ERP) work has indicated that the neural processing of action sequences develops with age. While adults and 9-month-olds use a semantic processing system, perceiving actions activates attentional processes in 7-month-olds. However, presenting a sequence of action context, action execution and action conclusion could challenge infants' developing working memory capacities. A shortened stimulus presentation of a highly familiar action, presenting only the action conclusion of an eating action, may therefore enable semantic processing in even younger infants. The present study examined neural correlates of the processing of expected and unexpected action conclusions in adults and infants at 5 months of age. We analyzed ERP components reflecting semantic processing (N400), attentional processes (negative central in infants; P1, N2 in adults) and the infant positive slow wave (PSW), a marker of familiarity.

~~The present study examined action processing in infants at 5 months of age and adults, using stimuli of reduced complexity when compared with prior studies. Specifically, rather than presenting a sequence of images depicting context, action execution, and action conclusion, the stimuli in the present study contained images of an expected or unexpected action conclusion only. ERP responses differed between conditions both in infants and adults.~~ In infants, the ~~positive slow wave (~~PSW~~)~~ was enhanced on left frontal~~o-parietal~~ channels in

response to ~~the~~ unexpected as compared to ~~the~~ expected outcomes~~ condition~~. ~~No differences between conditions were found for N400 or negative central (Nc) components, thus we~~We did not find differences between conditions in ERP waves reflecting ~~evidence for a~~ semantic processing or overt attentional mechanisms. In ~~our~~ adults~~ sample~~, in addition to differences in attentional processes on the P1 and the N2, an N400 occurred only in response to the unexpected action outcome, suggesting semantic processing taking place even without a~~n~~ complete action sequence being present. ~~The r~~Results indicate that infants are already sensitive to differences in action outcomes, although the underlying mechanism~~s~~ which is based on familiarity ~~, suggest that the cognitive systems employed are~~ is relatively rudimentary when contrasted with adults~~those utilized at older ages~~. This finding points toward different cognitive mechanisms being involved in action processing ~~at different time points~~ during development.

Keywords: action perception, event-related potentials, semantic processing, social cognition, N400, PSW

Introduction

The ability to detect, process and interpret human actions is perhaps one of the most complex components of social cognition. It is therefore remarkable that the capacity to engage with observed actions and identify actions as goal directed in nature is present in infancy~~. Much work has focused on the capacity of human infants to detect goals within actions~~ (see Gredebäck & Daum, 2015; Ní Choisdealbha & Reid, 2014 for an overview). ~~Behavioral work has indicated that infants at 6 months of age can detect that the goal is the defining element of an action by dishabituation to a change in the target of a reaching action when contrasted with a change of the path of a reaching action (Woodward, 1998). A critical and unaddressed issue remains from behavioral studies; namely that the capacity to dishabituate when detecting changes in goal directed behavior or, alternatively, anticipate the goal of an action, may be due to the use of different cognitive factors at various times in development.~~ A critical but mainly unaddressed issue remains; namely which processes, such as attentional or semantic processes, underlie action understanding at different ages. The current study ~~therefore~~ aims ~~at~~ to shed~~ding~~ light on the neural processes taking place during action perception in ~~developmental trajectory of action perception from~~ early infancy ~~to~~ and in adulthood. We examined neural correlates of the processing of expected and unexpected action conclusions in the context of food consumption, one of the first observed and experienced crucial actions in infancy.

~~Gredebäck and Daum (2015) specified four processes that take place during action perception. During the first two processes, the observer of an action is prepared for the action as he/she detects a socially relevant organism (identification) and his/her attention is covertly shifted to the upcoming state of this agent (priming). During the third phase (prediction) action outcomes may be anticipated. Action prediction is mostly studied using anticipatory looking behavior.~~ Infants are remarkably good at understanding other people's movements as goal directed actions (Gredebäck & Daum, 2015). Infants' action understanding has mainly been studied using behavioral measures such as looking times, pupil dilation or anticipatory looking. Infants start to anticipate the goal of a grasping action between 6 and 12 months (Falck-Ytter, Gredeback, & von Hofsten, 2006; Kanakogi & Itakura, 2011) and this ability is related to their own grasping skills (Kanakogi & Itakura, 2011). Similar results were found for food consumption. At 6 months at the latest, infants anticipate that a cup or a spoon will be brought to the mouth (Hunnius & Bekkering, 2010; Kochukhova & Gredebäck, 2010). Not only do infants at 6 months of age have expectations about the end state of an action they observe, they are also able to evaluate whether an expected consequence occurred or not. This process has mostly been assessed with measures that reflect violation of expectation. In the context of grasping, infants as young as 6 months of age show longer looking times if an action consequence does not match with their expectations raised by the physical appearance of a grasp (Daum, Vuori, Prinz, & Aschersleben, 2009) or with their expectation about other people's goals (Woodward, 1998). With regard to feeding actions, starting at 4 months of age, infants seem to be more surprised when the bowl of a spoon is placed on the back of another person's hand (unexpected action outcome) than in the person's mouth (expected action outcome), as indicated by differences in pupil dilation (Gredebäck & Melinder, 2010, 2011). Thus, infants very early in life possess the ability to anticipate and evaluate other people's goal directed actions. The above mentioned studies used behavioral measures to investigate infants' action understanding. These studies leave the question open on *how* infants detect and interpret goal directed actions. This limitation can be overcome using neurophysiological measures like event-related potentials (ERPs). ERPs have a high temporal resolution and consist of well-defined components reflecting different steps during stimulus processing including semantic processing, allocation of attention, or memory updating.

Critically, these processes may be active to a different degree at differing points in development (Reid et al., 2009).

With regard to action evaluation, the N400 event-related potential component ~~N400~~ has been related to semantic mismatch within adult populations when a perceived action violated expectations in a current context (see Amoruso et al., 2013 for an overview of the N400 in action contexts). An enhanced N400 was found in response to movie sequences of actions that included unexpected action outcomes in the context of eating (e. g. empty spoon put to mouth) as compared to expected outcomes (~~full~~ spoon conveying food put to mouth) (Reid & Striano, 2008). Another study presented images depicting the crucial stages of an action in sequence (Reid et al., 2009). Expectations about the action outcome were raised ~~within~~ by 2 images of an ongoing action (image 1 action context: e. g. a person holding a pretzel; image 2 action execution: a person bringing the pretzel to the mouth) while a third image presented either an expected action conclusion (the pretzel in the mouth of the person) or an unexpected action conclusion (the pretzel at the ear of the person). In adults, an N400 component was elicited only in response to the unexpected outcome, reflecting a mismatch in the semantic processing of this action. The same effect was found in 9-month-olds indicating that infants at this age anticipate the outcome of an expected or unexpected action via the use of semantic processing systems. However, no N400 effect was found with infants at 7 months of age, although the negative central (Nc) component, related to attention mechanisms (Reynolds, 2015; Reynolds & Richards, 2005), differentiated conditions (Reid et al., 2009).

One explanation for this finding is that younger infants do not utilize semantic systems during action processing. Rather, discrimination between conditions is due to mechanisms related to attention, which according to Reid et al. (2009) was reflected in differences in the Nc component. As the Nc component is associated with allocation of attention (Reynolds, 2015; Reynolds & Richards, 2005) and is enhanced for familiar when compared to unfamiliar stimuli in infants (de Haan & Nelson, 1999), the highly familiar and evolutionarily significant event of eating elicited more activation on this component (Reid et al., 2009). An alternative explanation is that younger infants found the paradigm, comprising a sequence of three images, to be too complex for optimal processing. The presented three-step sequence of action context, action execution and action conclusion may challenge infants' working memory capacity specifically at the younger age group (Ross-sheehy, Oakes, & Luck, 2003). This overload in information may inhibit semantic processing. It may therefore be possible that even infants younger than 9 months of age possess the ability to process action information in a semantic manner, but the rather complex paradigm may have been unsuitable to elicit evidence for this ability. In order to address this alternative explanation, the present study reduced the complexity of the stimulus presentation: instead of presenting the complete three-step sequence of context, execution and conclusion (as in Kaduk et al., 2016; Reid et al., 2009), we presented only the picture of the action conclusion to the infants. We assume that this simplified presentation facilitates the processing of the stimuli, as no other information (i.e., action context, action execution) need to be kept in mind to evaluate the end state of the action. This assumption is in line with studies showing that reducing the complexity of stimuli influences the neurophysiological processes taking place in ERP studies (Peykarjou, Pauen, & Hoehl, 2014, 2015). From a practical standpoint, it was anticipated that these single-image stimuli would be more likely to be tolerated by young infants than multiple-image sequences, resulting in better data quality and more trials for inclusion in ERP averages. In order to investigate neural correlates of early action understanding, we tested 5-month-olds. As behavioral results show, infants around this age are able to anticipate and evaluate eating actions (Gredebäck & Melinder, 2010, 2011; Hunnius & Bekkering, 2010; Kochukhova & Gredebäck, 2010), we therefore chose to examine 5-month-olds as we were particularly interested in the early neural correlates of action understanding, asking the question - is semantic processing already functioning when infants have just started to understand other people's actions, or do other processes, like attention, develop before semantic processing? Given that neural correlates of action perception have not been widely studied in a 5-month-old cohort, hypotheses for the infant sample included multiple possible neural correlates of action perception. If a less complex presentation of the action conclusion enables even younger infants to process the stimuli semantically, we hypothesized that an N400 would be found in response to the unexpected action conclusion. On the other hand, a lack of action understanding or the missing context may lead to no differences or to differences on a more basic processing level. This could be reflected in an enhanced Nc component for the expected condition indicating allocation of attention to the salient eating action (Reynolds, 2015; Reynolds & Richards, 2005) as it was the case in 7-, and 9-month-olds (Reid et al., 2009). Another plausible component to differentiate between conditions is the positive slow wave (PSW). Even though it has not previously been investigated in the context of action understanding in infants, it is related to memory updating processes of only partially encoded stimuli (Nelson, 1997; Riby & Doherty, 2009; Snyder, 2010; Snyder, Garza, Zolot, & Kresse, 2010; Webb, Long, & Nelson, 2005). An enhanced PSW for the unexpected condition would reflect the increased neural resources which are needed to encode this action outcome. This would conversely show that the expected action outcome is already more familiar to the infants. Differences on the PSW would inform us about infants' familiarity with the action outcomes. Any differences in these ERP components in response to the expected and unexpected action outcome stimuli could indicate whether the associated processes (N400: semantic processing, Nc: allocation of attention, PSW: familiarity) are functional during action processing at 5 months of age. Considering the results of the current study in addition to the prior literature related to the Nc and the N400 in 7- and 9-month-old infants (Reid et al., 2009) will provide us with informative insights into cognitive mechanisms taking place during action perception in the first postnatal year of life.

To further investigate the role of the context of an action, we also tested an adult sample with the same paradigm. As we kept the stimuli and the timing of the action conclusion pictures identical to Reid et al. (2009), comparing our results to the adult results in Reid et al. (2009) allowed us to directly examine the influence of the presented action context and action execution on the neural processing of expected and unexpected action conclusions. For the adult sample, we hypothesized the following - in line with Reid et al. (2009), we expected to find an N400 component in response to only the unexpected action conclusion in the adult sample (see also Mudrik, Lamy, & Deouell, 2010). As we presented photographic images of actions as stimuli, a frontal distribution of the N400 was expected (Amoruso et al., 2013; Ganis, Kutas, & Sereno, 1996). In the study by Reid et al. (2009), attentional mechanisms were involved in the processing of the stimuli in 7-, and 9-month-old infants as reflected in an Nc component of greater magnitude for the expected condition. This enhanced allocation of attention possibly indicated the high salience and evolutionary significance of the depicted eating action. In the adult sample, we therefore analyzed differences between conditions on the P1 component (Vogel & Luck, 2000) which is associated with arousal and the N2 component, which is associated with processes of orientation of attention and is suggested to be a successor to the infant Nc component (Folstein & Van Petten, 2008; Rothenberger, Banaschewski, Siniatchkin, & Heinrich, 2007).

~~Hunnius and Bekkering (2010) found that across all ages from 6 to 16 months of age, infants predicted that a cup would go to the mouth at least 25% of time with fewer than 5% of predictive looks towards the ear. This effect was reversed for a phone, indicating the presence of object knowledge and action effectors in early development.~~

~~One of the first tools infants are exposed to are spoons which infants start to use around 9 months of age (Connolly & Dalgleish, 1989; McCarty & Keen, 2005). Kochukhova and Gredebäck (2010) found that infants even prior to this age, at 6 months of age, anticipated that an actor would put a spoon to her own mouth. Older infants at 12 months of age predict this outcome even in a more complex two-person-interaction (Gredebäck & Melinder, 2010). Most interestingly, the authors show a direct relation between infants' ability to predict the feeding action and their feeding experience: infants' latency to predict the expected goal outcome (spoon ending in the mouth) was correlated with the days of their life experience of being fed. A similar result was found in the context of grasping. Infants' own grasping ability was positively related to the latency of predictive looks to a grasping action in 4-, to 10-month-olds (Kanakogi & Itakura, 2011).~~

~~According to the model proposed by Gredebäck and Daum (2015) the fourth and final process of action perception is the evaluation of the action outcome, i. e. the evaluation of whether an expected consequence of an action was reached or not. This process is mostly assessed with measures that reflect violation of expectation. With regard to feeding actions, already 6-month-olds seem to be surprised when, eventually, the spoon ends on the back of another person's hand (unexpected action outcome) instead of in the mouth (expected action outcome) as indicated by differences in pupil dilation (Gredebäck & Melinder, 2010). Most interestingly, this result was found in infants that do not yet use spoons themselves.~~

~~The results of these studies suggest that infants are able to predict and evaluate the outcomes of actions they observe frequently but do not yet perform (Gredebäck & Melinder, 2010; Kochukhova & Gredebäck, 2010). On the other hand, active action production indeed facilitates action perception (Gredebäck, Fikke, & Melinder, 2010; Kanakogi & Itakura, 2011; Sommerville, Woodward, & Needham, 2005). Taken together, the results of these studies raise important questions about the relationship between action perception and action~~

~~production. Clearly, there is an interplay between the perception and production of goal directed actions, but the ability to perform an action is not always required to predict its outcome. According to concepts of Common Coding (e. g. Daum, Prinz, & Aschersleben, 2008; Prinz, 1997) these aspects of cognition do function in isolation from each other, as well as in a combined manner. Studying the neural correlates of the perception of food-related actions in young infants (e.g. 5-month-olds) provides scope to understand how perceived actions that are familiar to the infant but not yet performed by him are encoded. Using the same paradigm and stimuli in adults allows for a better understanding on developmental trajectories.~~

~~A remarkable amount of knowledge has been gained with respect to action processing via behavioral and eye tracking studies in early development (see Ní Choisdealbha & Reid, 2014 for a review). One unanswered question is *how* infants detect and interpret goal directed actions. The measurement of overt behavior cannot fully address this issue. ERPs that are correlated with goal directed action, however, do have the capacity to inform on this topic. ERPs also have the ability to assess a number of cognitive processes simultaneously. Critically, each process may have little or no role to play at differing points in development. It is conceivable that differences in overt behavior throughout development are a consequence of entirely different underlying cognitive processes.~~

~~systems during action processing. Rather, discrimination between conditions is due to mechanisms related to attention, which according to Reid et al. (2009) was reflected in differences in the Nc component. As the Nc component is associated with allocation of attention (Reynolds, 2015; Reynolds & Richards, 2005) and is enhanced for familiar when compared to unfamiliar stimuli in infants (de Haan & Nelson, 1999), the highly familiar and evolutionary significant event of eating elicited more activation on this component (Reid et al., 2009). An alternative explanation is that younger infants found the paradigm, comprising~~

~~a sequence of images, to be too complex for optimal processing. In order to address this complexity issue as well as our aim to investigate the involvement of different mechanisms throughout development, the present study examined action processing during infancy at 5 months of age. Given the rate of development of action perception in infancy, 5-month-olds represent a participant group that is likely to process action outcomes differently to 9- and possibly 7-month-old infants. Research on goal perception by Woodward (1998) showed that 5-month-olds process actions in terms of goals, but their preference to look at goal violations was not as strong as that of the older, 9-month-old infants. Given that 5 months represents the earliest age, to date, at which goal processing is reported, determining the neural correlates of goal perception in this age group contributes to an understanding of how the cognitive processes are employed in goal perception change across the first postnatal year of life.~~

~~It is important to note that the current study utilized stimuli of reduced complexity when compared with prior studies. Specifically, rather than presenting a sequence of images depicting context, action execution and action conclusion~~ (as in Kaduk et al., 2016; Reid et al., 2009)~~, the stimuli that were presented in the current study consisted of images of action conclusion only. Although the stimuli used in this study differ from previous studies in this regard, results are likely to be comparable with the previous literature. This is because Kochukhova and Gredebäck (2010) and Hunnius and Bekkering (2010) have shown that infants who are only slightly older (6-month-olds) predict the outcomes of food-related actions based on actors' employment of food-related tools and objects. Thus, the creation of context prior to showing the critical stimulus is likely to be unnecessary. From a practical standpoint, it was anticipated that these single-image stimuli would be tolerated better by 5-month-olds than multiple-image sequences, resulting in better data quality and more trials for inclusion in ERP averages.~~

~~In summary, the aim of the present study was to investigate neural correlates of action evaluation in response to action conclusion alone, without the complex context of an action sequence in 5-month-olds and adults. In line with Reid et al. (2009), we hypothesized to find an N400 component in response to only the unexpected action conclusion in the adult sample (see also Mudrik et al., 2010). As we presented photographic images of actions as stimuli, a frontal distribution of the N400 was expected . Attentional mechanisms were involved in the processing of the stimuli in 7-, and 9-month-old infants as reflected in a higher Nc component for the expected condition (Reid et al., 2009). This enhanced allocation of attention possibly indicates the high salience and evolutionary significance of the depicted eating action. We therefore analyzed differences between conditions on the P1 component (Vogel & Luck, 2000) which is associated with arousal and the N2 component, which is associated with processes of orientation of attention and is suggested to be a precursor to the infant Nc component (Folstein & Van Petten, 2008; Rothenberger et al., 2007).~~

~~Given that the neural correlates of action perception have not been widely studied in a 5-month-old cohort, hypotheses for the infant sample included multiple possible neural correlates of action perception. If a less complex presentation of the action conclusion enables even younger infants to process the stimuli semantically, we hypothesized that an N400 would be found in response to the unexpected action conclusion. On the other hand, a lack of action understanding or the missing context may lead to no differences or to differences on a more basic processing level. This would be reflected in an enhanced Nc component for the expected condition indicating allocation of attention (Reynolds, 2015; Reynolds & Richards, 2005) as it was the case in 7-, and 9-month-olds (Reid et al., 2009). On a more rudimentary level, an enhanced PSW for the unexpected, thus unfamiliar, condition would reflect novelty detection and memory updating processes for partially encoded stimuli (Nelson, 1997; Riby & Doherty, 2009; Snyder, 2010; Snyder et al., 2010; Webb et al., 2005).~~

~~Such differences in these ERP components in response to the expected and unexpected action outcome stimuli could indicate whether the associated processes are functional during action processing at 5 months of age.~~

Method

Participants

All subjects were recruited following a local media campaign for volunteers, from the area in and around Stockton-on-Tees, North East England. This study was conducted with the understanding and the written consent of each participant's caregiver or the participant in accordance with institutional protocols.

Infants

The final analysis was comprised of the data of 15 5-month-old infants (average age: 152 days, range: 147 – 167 days; 11 male, 4 female). The sex of the infant participants was not equally distributed, but as we did not have any expectations about how the sex of the participants would influence the results, we have no reason to believe that this unequal distribution impacts the validity of our study. Another 7 infants (2 female, 4 male, 1 unknown) were tested but had to be excluded from the final sample because they failed to reach the minimum 10 artifact-free trials per condition (*n* = 5), or because of technical failure (*n* = 2). ~~On average each infant contributed a mean of 31 trials (*SD* = 12.95) to their average for the expected conclusion of the action condition and a mean of 32 trials (*SD* = 14.48) for the unexpected conclusion of the action condition.~~ All infants had to be ~~were~~ born full term (37-42 weeks gestation). No other exclusionary criteria were applied. Infants were given a t-shirt and £10 was given to the parents to cover travel costs.

Adults

The adult sample consisted of 27 adults who were undergraduate students with normal or corrected to normal vision. ~~Analyses relied on a mean of 99 trials in the unexpected (*SD* = 25.99) and 99 in the unexpected condition (*SD* = 25.09) with a minimum of 25 and 28 included trials, respectively.~~ All tested adults were included in the final analyses. Adult subjects received £7 to participate.

Stimuli

The stimuli were photographs depicting a male or a female actor, showing eating actions in two different ways: either with a spoon or holding the food. Those actions were presented either in an *expected* manner (food in mouth) or in an *unexpected* way (food touching other parts of the head). Figure 1 shows all stimulus pictures that were used in the study. Each infant saw each of the eight different stimuli. Stimuli were presented at full screen size (26 cm ~~X~~x 34 cm) on a 60 Hz 17-inch height adjustable stimulus monitor at a viewing distance of 90 cm. This produced a visual angle of 16.44° x 21.39°.

Figure 1: Stimulus material ~~depicting~~ used in the study~~eating~~. Top line displays the expected action; bottom line displays the unexpected action both for the male and female actor. Note: images were displayed in color to participants.

Procedure

During recording, infants sat on their caregiver's lap in a dimly lit 2 x 2 metre testing area which was separated from the rest of the laboratory by black colored room dividers. A camera located above the center of the presenting screen recorded infants' looking behavior. If an infant became fussy or uninterested in the stimuli, the experimenter gave the infant a short break and attempted to resume the study when the infant was once again alert and calm. The testing session ended when the infant's attention could no longer be attracted to the screen. EEG was recorded continuously during the presentation.

The experiment consisted of a block of 32 action conclusion photographs with a division of male-female stimuli and expected-unexpected trials of exactly half each. The block could be repeated 9 times resulting in a maximum of 288 stimulus presentations. The two conditions were presented to the ~~subject~~ participant in a pseudo-randomized order with the constraint that the same condition was not presented more than three times consecutively.

Stimuli were presented utilizing the *Stim²-Gentask* computer software package by Neuroscan Compumedics (Charlotte, USA).

Each ERP time-locked image was presented on the screen for 1000 ms. Between the presentation of each image, the screen was white for a period of 700 ms only displaying a fixation cross in the center of the screen (see Figure 2 for an example of the stimulus presentation sequence). A 1700 ms period in between the onset of one critical stimulus and the next was used based on previous work with infants by Friedrich and Friederici (2011).

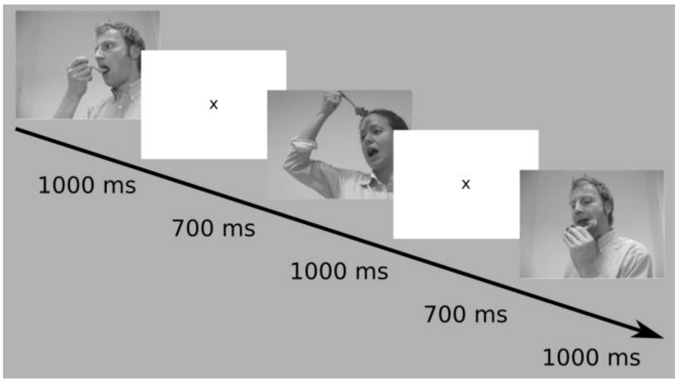

Figure 2: An example of the stimuli sequence presented to the participants: From top left to bottom right: expected-spoon *(1000 ms)*, inter-stimulus-interval *(700 ms)*, unexpected-spoon *(1000 ms)*, inter-stimulus-interval *(700 ms)*, expected-holding food.

EEG Recording and Analysis

EEG was recorded continuously from 32 scalp locations according to the 10-20 system, referenced online to AFz using Ag-AgCl ring electrodes with a sampling rate of 1Khz. For infants, the quality of the ongoing EEG data was inspected visually, and individual electrodes were examined if required, with the application of more paste should an electrode be too noisy or displaying channel offsets. For the adult sample, impedances were kept lower than 10 kΩ. Horizontal and vertical electro-oculograms (HEOG+ and VEOG+) were recorded bipolarly and the EEG data was amplified via a Neuroscan 32-channel amplifier. For additional data editing, the software EEGLAB version 13.4.4b was used (Delorme & Makeig, 2004). Raw data ~~was~~ were filtered offline with a 0.3 to 30 Hz bandpass filter using the pop_eegfiltnew function in EEGLAB and re-referenced offline to the averaged mastoids (TP9, TP10). Data were segmented into epochs of waveform that comprised 200 ms prior to stimulus onset and 1000 ms following stimulus onset. Baseline was corrected using the 200 ms before stimulus onset. Following review of the video recordings of infant behavior, all trials in which the infant did not pay attention to the stimuli for the full 1000 ms of stimulus presentation were rejected from further analysis. On average, this included 53 trials in the expected (range of 24 – 99 trials) and 50 (range of 20 – 101 trials) in the unexpected condition in the infant sample. No significant difference between the amount of trials rejected based on the video analysis in the expected and in the unexpected condition were found, $t(14) = 1.49$, $p = 0.159$. The majority of trials was rejected because infants did not attend to the trials at all (mean of 37 trials in the expected and mean of 35 trials in the unexpected condition). In contrast, it was only in the minority of the excluded trials that infants attended to the trials at some point but not during the whole 1000 ms (mean of 16 trials in the expected and mean of 15 trials in the unexpected condition). For both measures (amount of trials infants did not attend to the screen at all and amount of trials infants only paid attention to the stimulus at some point during the stimulus presentation), we did not find differences between both conditions, $t(14) = 1.49$, $p = 0.159$ and $t(14) = 0.54$, $p = 0.596$, respectively. All remaining trials were scanned for artifacts using the automatic artifact detection implemented in ERPLAB version 5.0.0.0 (Lopez-Calderon & Luck, 2014). A trial was excluded from further analysis whenever the peak-to-peak amplitude in any channel exceeded a threshold of 200 µV in a 200 ms window. Window steps were set to 100 ms (Wahl, Michel, Pauen, &

Hoehl, 2013). The remaining segments were visually and manually edited for artifacts and blinks. Finally, data were averaged for the expected and the unexpected condition.

On average each infant contributed a mean of 31 trials (*SD* = 12.95, range 15-54) to their average for the expected conclusion of the action condition and a mean of 32 trials (*SD* = 14.48, range 13-66) for the unexpected conclusion of the action condition.

For the adult sample, ~~A~~analyses relied on a mean of 99 trials in the unexpected (*SD* = 25.99, 25-135) and 99 in the unexpected condition (*SD* = 25.09, range 28-136) with a minimum of 25 and 28 included trials, respectively.

Results

The level of significance was set to 0.05 if not stated otherwise and Greenhouse-Geisser correction was applied if applicable. Grand average of all channels for the infant sample can be found in Supplementary Material 1.

Infants

N400

Although an N400 analysis might have been pursued on the basis of previous work (Reid et al., 2009) and to establish whether the simplified stimuli would elicit such an effect in a younger age group, visual inspection did not show any evidence for an N400 (Figure 3). ~~To further test for an N400 effect in our sample, we conducted the same analysis as with the infant participants in Reid et al.'s action observation study.~~ In the 9-month-olds in Reid et al. (2009), the N400 component was present in the unexpected condition and absent in the expected condition. To detect such differences in the morphology between ERP waves, for example the presence of a component in one condition and the absence of a component in the other condition, an analysis, as described by Hoormann, Falkenstein, Schwarzenau, and

Hohnsbein (1998), can be performed. To conduct this analysis, the values of the amplitude of the ERP wave are extracted at several time points for both conditions and compared in a repeated measures ANOVA with within-subject factors of time and condition. If ERP waves differ in their morphology, the interaction between the factors time and condition will reach significance. To ~~further~~ test for an N400 effect in our sample, we conducted the same analysis as with the infant participants in Reid et al.'s (2009) action observation study. However, we included only 15 instead of 17 time windows to be able to appropriately estimate the parameters given our sample size. Using the same time window (612 to 780 ms) and the same electrodes (P3, Pz, P4), a 2 x 15 repeated measures ANOVA with the within-subjects factors condition (expected vs. unexpected) and time (15 samples at one per 12 ms) was performed. ~~as suggested to detect differences in the morphology of ERP waves by~~ Hoormann et al. (1998)~~.~~As the signal of some participants may cross the x-axis in the selected time window, data were normalized for each participant and each condition using the following quotient to calculate the values for each time point

$$\textit{value at each time point} = \frac{\textit{mean amplitude}}{\textit{normalization}}$$

with

$$\textit{mean amplitude} = \textit{mean value of } P3, Pz \textit{ and } P4 \textit{ for this time point}$$

$$\textit{normalization} = \frac{\sum \textit{normalized mean amplitudes of all time points}}{\textit{number of time points}}$$

$$\textit{normalized mean amplitude}$$
$$= \textit{mean amplitude of each time point}$$
$$- \textit{minimal amplitude of all time points of this participant and condition}$$

Field Code Changed

~~(mean amplitude averaged of all selected channels for each time point) / (sum of (data at each time point – minimum value of all time points) / number of time points).~~

A significant time x window interaction would indicate a difference in morphology. No condition x time interaction was found, *F*(3.0~~9~~0, 4~~3~~2.~~31~~01) = 1.~~59~~47, *p* = 0.2~~0~~36.

Infants' initial expectations about the presented eating action may have been overwritten by repeatedly seeing a person holding food to the head in the course of the experiment. To test for this idea, we performed the same analysis only for the first half of valid trials for infants that contributed more than 20 trials to each condition. This analysis included 11 infants. No significant condition x time interaction was found, *p* = 0.547.

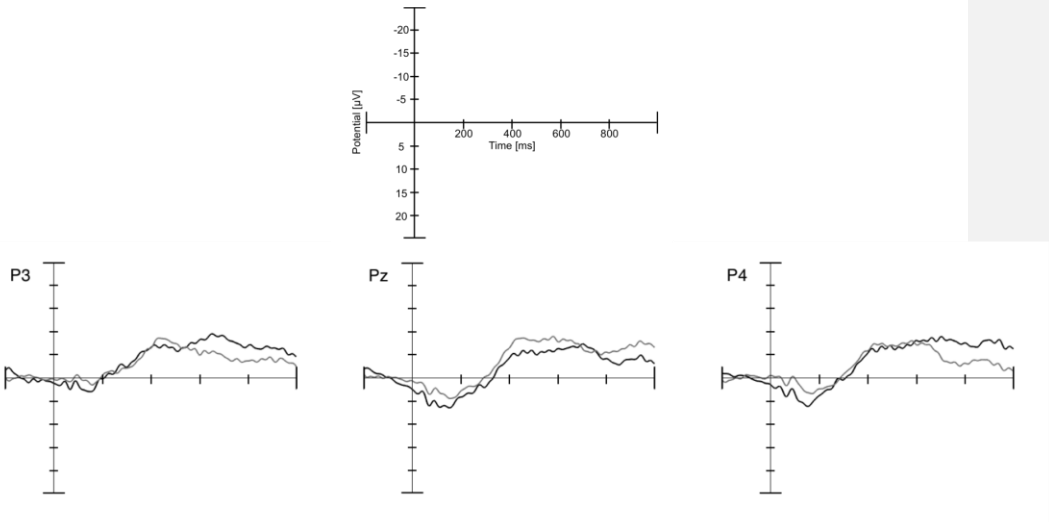

Figure 3: Channels analyzed for the N400 component in the infant sample. Black lines show the expected and grey lines refer to the unexpected condition. Note that negative is plotted up.

Nc

The mean amplitude for the Nc was assessed in left fronto-central (FP1, F3, FC5 and C3), fronto-central (Fz and Cz) and right fronto-central (FP2, F4, FC6 and C4) electrode clusters in a time window between 350 – 600 ms after stimulus onset, which fitted the resultant morphology and was ~~in~~ congruent~~ce~~ with other studies investigating this waveform (Hoehl, Reid, Mooney, & Striano, 2008; Kaduk et al., 2016). A 2 x 3 repeated measures ANOVA was conducted with the within-subjects factors condition (expected vs. unexpected) and region of interest (left vs. central vs. right). This analysis revealed only a significant interaction between condition and region of interest, $F(1.39, 19.50) = 5.27$, $p = 0.024$, $\eta_p^2 = 0.273$, all other *ps* > 0.321. As post hoc repeated measures ANOVAs confirmed, this interaction was due to differences in the amplitude between the regions of interest only in the expected condition ($F(2,28) = 6.50$, $p = 0.005$, $\eta_p^2 = 0.317$). No such difference was found for the unexpected condition, $p = 0.879$. Level of significance for post hoc ANOVAs was set to $p < 0.025$. Follow-up paired t-tests revealed that amplitude over the left hemisphere in the expected condition was more negative than over the right hemisphere, $t(14) = -3.671$, $p = 0.003$. When comparing the expected and unexpected conditions separately for each region of interest with paired t-tests, no significant difference was found, all *ps* > 0.061. Level of significance for the post hoc paired t-tests was set to $p < 0.017$ for Bonferroni correction.

PSW

The 650 – 900 ms time window for the PSW analysis was selected due to the morphology of the data. Although this time window is shorter and earlier than the PSW window typically used in other studies (de Haan & Nelson, 1997; Webb et al., 2005), visual inspection of the data (see Figure 4) showed the slow wave tapering off before 1000 ms post-stimulus. Data were analyzed accordingly and in ~~congruence~~ accordance with procedures used in other studies reporting earlier PSW effects (Reid, Striano, Kaufman, & Johnson, 2004; Striano, Kopp, Grossmann, & Reid, 2006) and hemisphere specific differences (Csibra, Tucker, & Johnson, 2001; Parise, Friederici, & Striano, 2010; Parise, Reid, Stets, & Striano, 2008; Reid et al., 2004). A 2 x 2 repeated measures ANOVA with within subject factors condition (expected vs. unexpected) and hemisphere (right vs. left) was conducted with the mean amplitude on left (FP1, F3, FC5, C3, CP5) and right (FP2, F4, FC6, C4, CP6) frontal~~o-parietal~~ channels in a time-window of 650 – 900 ms. Channels were chosen with regard to visual inspection of the grand averages and the existing literature showing that the PSW is most prominent on fronto-temporal electrodes (de Haan & Nelson, 1999; Reid et al., 2004; Snyder, Webb, & Nelson, 2002)

Results revealed no significant main effect of condition, $p = 0.134$, however a significant main effect of hemisphere was found, $F(1,14) = 8.10$, $p = 0.013$, $\eta_p^2 = 0.367$. The interaction between hemisphere and condition showed a significant effect, $F(1,14) = 6.13$, $p = 0.027$, $\eta_p^2 = 0.305$. Level of significance for post hoc tests comparing both conditions separately for the left and the right hemisphere was set to $p < 0.025$ for Bonferroni correction. Paired sample t-tests revealed that conditions differed significantly from each other only over~~n~~ the left hemisphere $t(14) = -2.56$, $p = 0.023$, $d = 0.660$, not over~~n~~ the right hemisphere, $t(14) = -0.211$, $p = 0.836$, $d = 0.055$. Over~~n~~ the left hemisphere, mean amplitude was more positive for the unexpected condition (mean = -6.36, SE = 2.05) as compared to the expected condition (mean = -10.92, SE = 2.20). No such difference was found o~~n~~ver the right hemisphere (mean = -5.29, SE = 2.34 for the unexpected condition and mean = -5.66, SE = 2.34 for the expected).

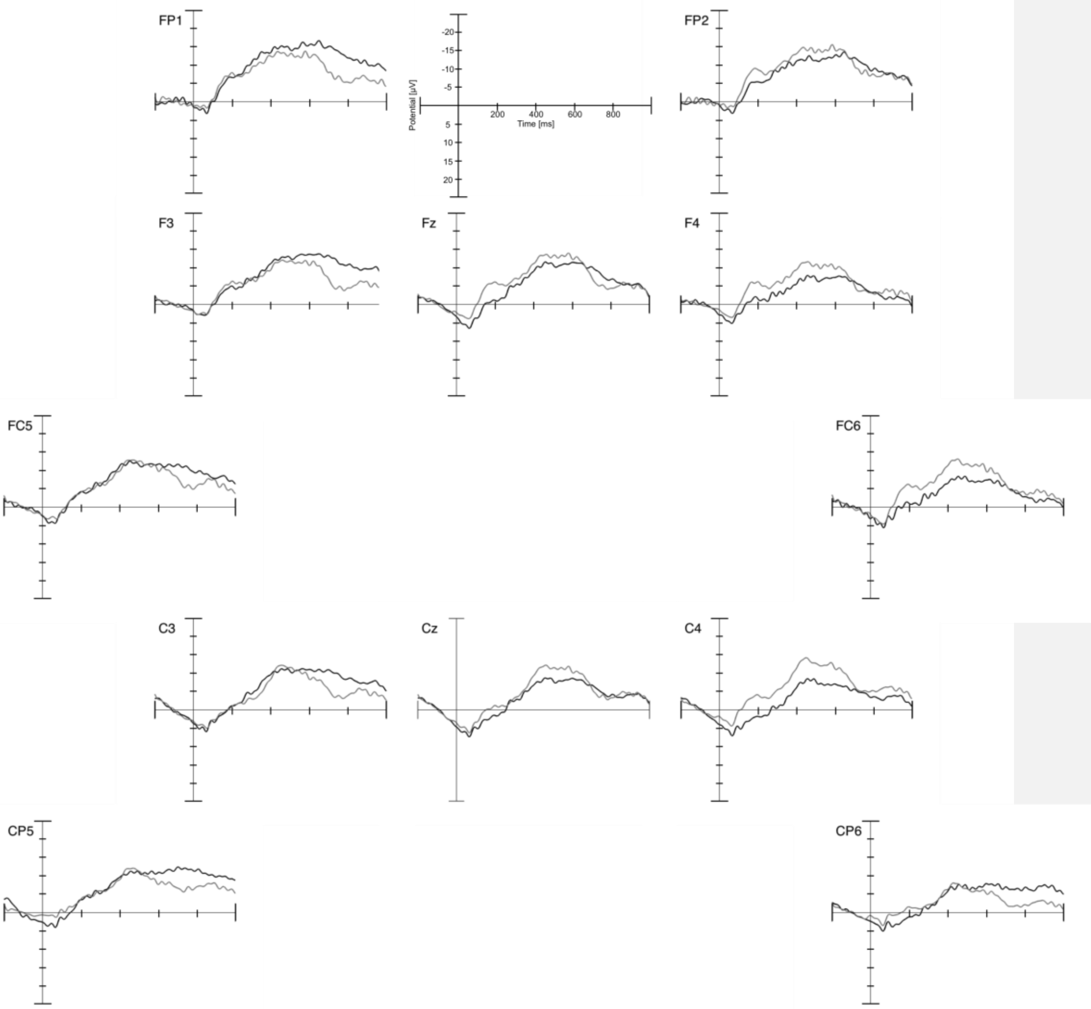

Figure 4: Channels analyzed for the Nc~~C~~ and PSW in the infant sample. Black lines show the expected and grey lines refer to the unexpected condition. Note that negative is plotted up.

Adults

The level of significance was set to 0.05 if not stated otherwise and Greenhouse-Geisser correction was applied if applicable. Grand average of all channels for the adult sample can be found in Supplementary Material 2.

N400

As in Reid et al. (2009) the N400 component was only visible in the unexpected condition, whereas no N400 was visible in the expected condition. To test EEG data for differences in morphology between conditions, Hoorman, Falkenstein, Schwarzenau, and Hohnsbein (1998) suggest~~ed~~ a window analysis. Therefore we exported in total 13 amplitude values every 12 ms between 400 – 544 ms over~~n~~ fronto-central channels (FP1, FP2, F3, Fz, F4, F7, F8, FC5, FC6, C3, Cz, C4) where the N400 was most prominent~~-~~(Amoruso et al., 2013; Ganis et al., 1996; Reid et al., 2009). Again, as the signal of some participants may cross the x-axis in the selected time window, data were normalized for each participant and each condition using the same normalization quotient as for the infant data. ~~of (mean amplitude averaged of all selected channels for each time point) / (sum of (data at each time point – minimum value of all time points) / number of time points).~~ A repeated measures ANOVA with the within-subject factors condition (expected vs. unexpected) and time (13 time points) was conducted. A significant condition x time interaction would suggest that the ERP waves differ between conditions, for example that the N400 would be present in only one condition. The ANOVA revealed a significant condition x time interaction, $F(3.84, 99.93) = 3.06$, $p = 0.022$, $\eta_p^2 = 0.105$. This significant interaction between condition and time highlights that there are differences in the morphology between the ERP waves of the two conditions. As can be seen in Figure 5, the N400 was only present in the unexpected condition but not in the expected. No main effects were found, all $ps > 0.069$.

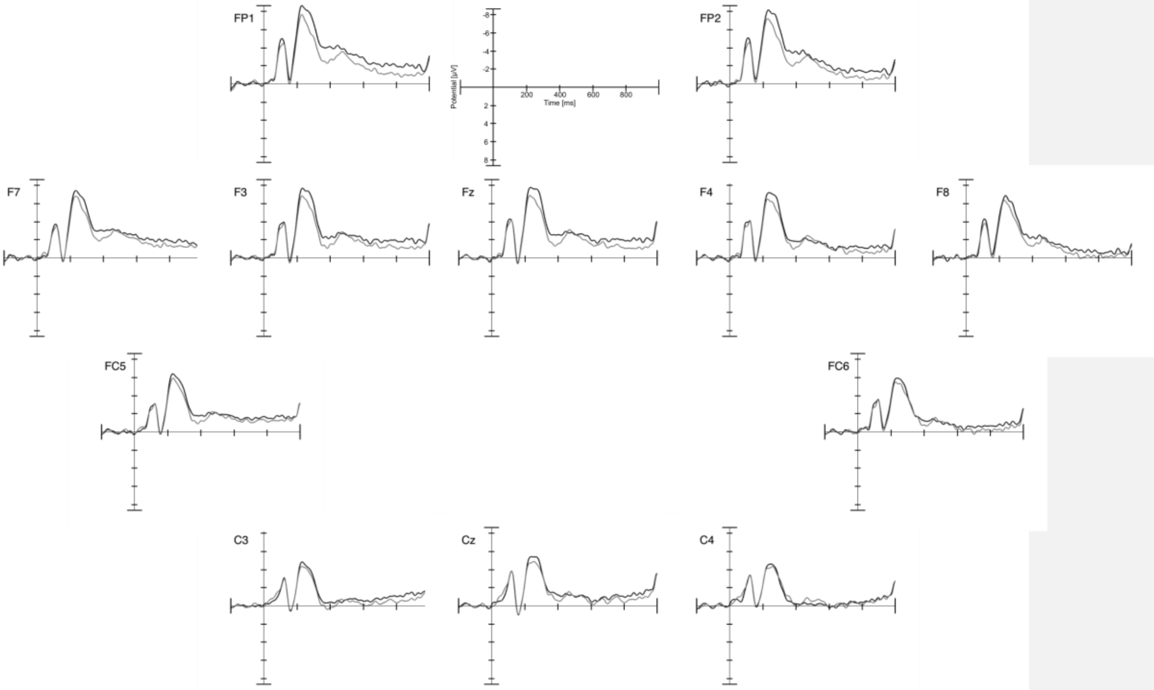

Figure 5: Channels analyzed for the N400 and the N2 component in the adults sample. Black lines show the expected and grey lines refer to the unexpected condition. Note that negative is plotted up.

P1

The visual component P1 is known to appear 80-130 ms after stimulus onset on occipital areas (Hillyard & Anllo-Vento, 1998). To investigate effects on the P1, mean amplitudes on left (O~~0~~1 and PO9) and right (O2 and PO10) occipital channels in the time-window 80-130 ms served as the dependent variable. A 2 x 2 repeated measures ANOVA with the within-subject factors condition (expected vs. unexpected) and hemisphere (left vs. right) only yielded a significant main effect of condition, $F(1,26) = 5.83$, $p = 0.023$, $\eta_p^2 = 0.183$, with a more positive amplitude for the expected condition (mean = 3.71, SE = 0.44) than for the unexpected condition (mean = 3.27 SE = 0.40). No other main effect or interaction was found, all *p*s > 0.428.

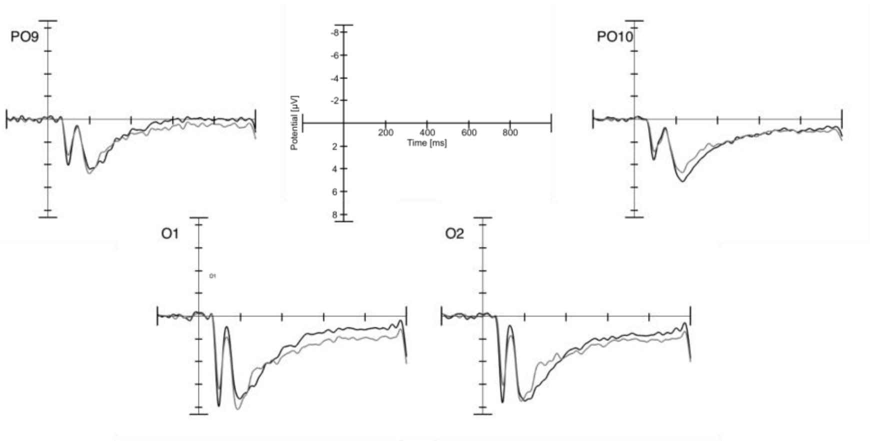

Figure 6: Channels analyzed for the P1 component in the adult sample. Black lines show the expected and grey lines refer to the unexpected condition. Note that negative is plotted up.

N2

The N2 component was analyzed on fronto-central left (FP1, F7, F3, FC5 and C3), fronto-central (Fz and Cz) and fronto-central right (FP2, F8, F4, FC6, C4) electrode clusters in the time-window 200-350 ms (Folstein & Van Petten, 2008). A 2 x 3 repeated measures ANOVA with the within-subject factors condition (expected vs. unexpected) and region of interest (left vs. central vs. right) only yielded a significant main effect of condition, $F(1,26) = 9.71$, $p = 0.004$, $\eta_p^2 = 0.272$, with a more negative mean amplitude for the expected (mean = -5.15, SE = 0.41) than for the unexpected condition (mean = -4.44, SE = 0.35). All other *ps* > 0.292.

Discussion

In this study, we examined the neural correlates that were associated with the perception of ~~the completion of an action in an~~ expected or unexpected action conclusions ~~manner~~ in early infancy and adulthood. In infants, the present experiment found that the PSW, but ~~neither~~ not the N400 ~~n~~or the Nc, differentiated expected and unexpected action outcomes at 5 months of age. The PSW -was ~~showed a difference in manifestation, with the unexpected condition displaying an~~ enhanced for the unexpected condition ~~PSW than~~ relative to the expected condition on left frontal~~o-parietal~~ channels. As the PSW is related to memory updating processes for stimuli that are only partially encoded (Nelson, 1997; Riby & Doherty, 2009; Snyder, 2010; Snyder et al., 2010; Webb et al., 2005), the result suggests that enhanced activity was required to process the unexpected, thus unfamiliar action conclusions when contrasted with processing the expected, more familiar ones. Infants ~~This suggests that infants~~ are sensitive to differences in action outcomes in early development. But ~~, although~~ the mechanisms by which this is displayed indicate that the cognitive systems employed are relatively rudimentary, as they are based on familiarity and memory encoding processes. ~~when contrasted with those utilized at older ages.~~ In adults, an enhanced N400 component occurred only in response to the unexpected action outcome, suggesting semantic processing of this action type even without the context of an action sequence being present. Results on the P1 and the N2 components indicate that attentional processes are active in adulthood similar to 7- and 9-month-old infants (Reid et al., 2009), at least when observing actions that are related to food consumption.

In our infant sample, no N400 component was produced for the unexpected condition when contrasted with the expected condition, even when we analyzed only the first half of trials to check for potential learning effects during the course of the experiment. There is currently some evidence that infants at 9 months of age use semantic systems to process actions (Kaduk et al., 2016; Reid et al., 2009) ~~(Reid et al., 2009)~~, although no such studies have been conducted ~~on~~ with infants as young as those investigated in the current study. In Reid et al. (2009), the complexity of the stimuli may have been one potential cause for a lack of N400 effect found in infants at 7 months of age. The present study attempted to simplify the stimuli yet aimed to still contain violations of expectation related to action outcomes in one condition but not the other. Despite simplification of the stimuli to facilitate processing, no N400 component was found. One explanation of this finding is, that ~~This suggests that~~ 5-month-old infants do not utilize semantic systems when observing other~~'~~s' action outcomes. Another possible explanation for the lack of an N400 effect is that infants need an action context and need to perceive how an action is executed to semantically process that action. To test this idea, one could test 5-month-olds with the three-step action sequence presentation present in Reid et al. (2009). Given that even 7-month-olds did not show signs of semantic processing in that paradigm, we would not expect N400 effects to occur. Another possibility for future research would be to examine 7- and 9- month-olds with our simplified paradigm. This way, the influence of the complexity of the stimulus presentation could be tested against the influence of embedding an action outcome into an action sequence.

Despite the lack of an N400 effect, ~~T~~the ERP waveform showed other components of interest in relation to infant processing of actions. The~~A~~ Nc component was observed in the morphology of the ERP waveform in both conditions ~~in the present study,~~. The mean amplitude of the Nc in both conditions differed significantly from baseline with $t(14) = -3.652$, $p = .003$ for the expected condition and $t(14) = -6.164$, $p \leq .001$ for the unexpected condition. H~~h~~owever, there was no statistical~~ly~~ difference in the mean amplitudes of the Nc between conditions. This is in contrast to the results found in 7- and 9-month-olds that showed an enhanced Nc component in response to the expected condition that was related to eating (Reid et al., 2009) and consequently in contrast to our hypothesis. One possible explanation for this lack of difference in the Nc component may be that the mere presence of food itself elicits allocation of attention in 5-month-olds, whereas 7-month-olds are already more sensitive to the action of actually *eating* food instead of the mere presence of food. As the Nc was equally distinct in both conditions, we cannot conclude that attentional mechanisms play no role in action understanding in young infants. However, our results show that attentional mechanisms did not discriminate between expected and unexpected goal outcomes.

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~~This suggests that there was no difference between conditions with respect to the use of overt attentional mechanisms when observing these different actin outcomes. This is in contrast to the results found in 7- and 9-month-olds that showed an enhanced Nc component in response to the expected condition that was related to eating (Reid et al., 2009).~~

In the present work, the mean amplitude of the PSW differed between conditions over~~n~~ frontal~~o-parietal~~ channels of the left hemisphere. The fact that the PSW differed between conditions only over~~in~~ the left hemisphere ~~stands in line~~ aligns with studies that have previously reported left frontal ERP effects in infancy from 4 to 6 months of age (Csibra et al., 2001; Parise et al., 2010; Parise et al., 2008). The PSW has been related to ~~novelty~~ familiarity detection, as it decreases with increased exposure to a stimulus (Snyder, 2010; Snyder et al., 2010) and ~~to~~when updating a memory representation of a partially encoded stimulus (Nelson, 1997; Webb et al., 2005). In the current study, the PSW was enhanced in response to the unexpected as compared to the expected condition. Thus, more activity was needed to encode the unexpected action outcome than the expected action outcome. This suggests that the unexpected action conclusion ~~This outcome~~ was most likely perceived as more novel and unfamiliar to the infants, whereas the expected outcome was already ~~more~~ familiar ~~stimulus to the infant brain~~ and therefore elicited less prominent slow wave activity. The result on the PSW analysis suggests that infants at 5 months of age process actions at the level of familiarity vs. novelty. It is therefore possible that differences in the PSW only occurred because infants were perceptually more familiar with food in the mouth than food at the head. It follows that this unfamiliarity elicited the enhanced PSW in the unexpected condition without awareness of what defines the novelty of this stimulus, that is, that the displayed action is unusual.

~~As stated above, no difference between conditions on the Nc component were found, whereas the PSW response differed between conditions. The Nc reflects an overt allocation of attention to a stimulus that the infant perceives as different from other stimuli. The PSW is likely to be a more basic response that might be compared to the prevention of habituation – the infant detects a difference in the stimuli presented without awareness of what the difference is. The outcome of the present study suggests that action outcomes at 5 months of age are monitored at this relatively rudimentary level of processing with a stronger response to the unexpected condition.~~

The findings of the present study help to refine our knowledge of action understanding in early development and suggest that other processes precede semantic processing of action. These processes, as shown in the present study and in previous work (Reid et al., 2009), are likely to involve detection of familiarity and, later in development, allocation of attention to the presented stimuli. ~~Although not directly addressed in the present study, other theories propose that early understanding of action is facilitated by imitation and motor resonance (Marshall & Meltzoff, 2011). The current study suggests that an understanding is now required for how attentional processes give rise to semantic processing~~

~~of action in later development, and for how motor resonance theories of action relate to the processes uncovered in this and related studies in early infancy. Even though f~~Further work is required to understand the earliest emergence of the semantic processing system and how its application to action processing corresponds to its application in language processing (Kaduk et al., 2016). ~~the current study points towards those factors most likely to prove fruitful in future research.~~

It is assumed that the reduction in complexity of the stimuli in the present study when contrasted with those used in Reid et al. (2009) will help to facilitate infant processing of the difference between expected and unexpected actions. This has not been verified via any independent means, such as assessing overall looking time or gaze shift patterns. Combining neurophysiological and behavioral measures would allow us to depict the broader picture of processes taking place during action understanding. A simultaneous application of both measurements very often seems impractical as different measures have different requirements (e.g. different timing of stimuli for different measures, required number of trials). Nonetheless, using the same stimuli in paradigms with different methods may be a promising next step for future research (Hoehl, Wahl, & Pauen, 2014; Wahl et al., 2013). For instance, an increase in pupil dilation in response to the action outcomes presented with and without the action context would inform us about the role of the presented action context for infants action understanding (Gredebäck & Melinder, 2010). Such combined methods are currently under development and, despite added complexities, stand to yield a number of advances in infancy research (Domínguez-Martínez, Parise, Strandvall, & Reid, 2015; Wass, de Barbaro, & Clackson, 2015).

In the present study, food stimuli were used because 5-month-old infants are familiar with feeding actions and observe their caregivers performing those actions multiple times daily. It is currently an open question whether other familiar but less motivationally salient object-directed actions, such as the phone- and hairbrush-related actions used in Hunnius and Bekkering (2010), elicit similar or distinct patterns of neural activity in infants of this age group. If the PSW effect in the present study was mainly driven by perceptual familiarity with the action, we would expect similar results to other actions which infants are familiar with.

As we kept the stimuli and the timing of the action conclusion picture identical to the study by Reid et al. (2009), adult results of both studies can be directly compared. In our adult sample, ~~adults,~~ an N400 occurred only in response to the unexpected action outcome, reflecting the processing of a semantic mismatch for the familiar action condition. This result is in line with studies that found an enhanced N400 in response to unfamiliar or unexpected action outcomes using video stimuli (Reid & Striano, 2008; Sitnikova, Holcomb, Kiyonaga, & Kuperberg, 2008) or pictures (Mudrik et al., 2010). It replicates the results of Reid et al. (2009) and therefore suggests that no action context is needed for adults to process actions in a semantic way.

In addition to the effects on the N400, enhanced P1 and N2 amplitudes were found in response to the expected condition. As stimuli were controlled for luminance, we do not consider that these differences are due to psychophysical characteristics. However, an increased P1 is associated with higher arousal (Vogel & Luck, 2000). The N2 is associated with an orientation of visual attention in oddball paradigms (Folstein & Van Petten, 2008). The fact that both components are enhanced for the expected condition (related to eating) is in line with the infant results in Reid et al. (2009) showing an enhanced Nc component, indicating more allocation of attention, to the expected action. In accordance with the interpretation of Reid et al. (2009), an eating action is a highly salient event and of high evolutionary significance that may therefore lead to more arousal and attention than the unexpected condition. Interestingly, the similarities in the function and the assumed neural source of the N2 and the Nc led to the suggestion that the Nc may be a precursor in infants to the adult N2 (Rothenberger et al., 2007). This may explain the analogous results -~~, thus~~ the enhanced activity for the expected condition~~,~~ - in our adult sample and the infant sample in Reid et al. (2009). However, see Marinović, Hoehl, and Pauen (2014) for a study that did not find corresponding results for infants and adults on the N2 in ~~their~~ an oddball paradigm.

As the paradigm in our study and the one used in Reid et al. (2009) differ in the substantial aspect of generating a complete context of an action including the execution of the context itself, direct comparisons of both studies are not valid except with the adult participants. ~~Taken together, t~~However, when taking the differences in the paradigm into account, the results from the current study ~~a~~when~~s~~ combined with the results by Reid et al. (2009) give us insight into ~~the developmental trajectories of~~ the neural mechanisms underlying action perception in the first postnatal year of life and in adulthood. When presented with only an action conclusion~~First~~, the infant brain~~s~~ at 5 months of age detects differences between ~~process~~ expected and unexpected action outcomes. ~~differently via encoding activity for the unexpected condition,~~This is likely due to familiarity, as ~~seen~~ shown by differences in the PSW. At 7 months, action ~~anticipation~~ understanding is indexed via differences in attentional mechanisms, as evidenced by changes in the Nc (Reid et al., 2009) in the context of an action sequence. Finally, at 9 months of age, in addition to the enhanced attention to the salient eating stimulus, the N400 is present when a complete action sequence is presented. This ~~reflects~~ indicates that semantic processing is involved in the processing of actions in a way that it continues into adulthood. For adults, even the presentation of the final action conclusion is sufficient for a semantic system to be activated in the detection of an unfamiliar action. The utilization of ERPs enabled us to disentangle the different underlying processes that drive action understanding at different points during development. Testing different age groups with the same paradigm in future studies, for example testing 7- and 9-

month-olds with our simplified stimuli, will help to disentangle the influence of the complexity of the presentation and the influence of the action context. ~~Thus, a general timeline of the behavioral and neural development of action processing can be detected in studies utilising ERP methodology. The proposed developmental trajecory fits the concept of redescription as outlined by Karmiloff-Smith (1992) whereby development can be characterized by an increasingly explicit, and more complex, cognitive architecture.~~

~~Intriguingly, this work suggests that differences in early development related to action perception that appear to be unidirectional at the behavioral level (e.g., Woodward, 1998) may be driven by entirely different cognitive mechanisms at discrete points during the first postnatal year . Our study suggests that results on action perception in behavioral studies in early infancy are most likely driven by simple mechanisms while more complex competences emerge over time.~~

~~It should be noted that it is assumed that the reduction in complexity of the stimuli in the present study when contrasted with those used in Reid et al. (2009) will help to facilitate infant processing of the difference between expected and unexpected actions. This has not been verified via any independent means, such as assessing overall looking time or gaze shift patterns. Other studies investigating similar ages have, however, found behavioral differences in the processing of different action categories with infants aged 5-6 months (e.g., Hunnius & Bekkering, 2010; Luo & Baillargeon, 2005). We therefore propose that it is not unreasonable to suggest that infants at 5 months of age would be capable of processing the stimuli used in the present study. In the present study, food stimuli were used because 5-month-old infants are familiar with feeding actions and observe their caregivers performing those actions multiple times daily. It is currently an open question whether other familiar but less~~

~~motivationally salient object-directed actions, such as the phone- and hairbrush-related actions used in Hunnius and Bekkering (2010), elicit similar or distinct patterns of neural activity in infants of this age group.~~

In conclusion, the results of this study demonstrate that infants at 5 months of age are capable of discriminating expected and unexpected actions, and that this is manifested at the level of neural activity. The finding that PSW was involved in this dissociation between conditions rather than other components which index ~~more complex~~higher levels of processing, such as attention or semantics, suggest that at 5 months of age infants utilize a relatively simple mechanism for detecting such differences based on familiarity. How this capacity relates to more complex forms of action processing, such as grasping the concept of affordance for tools as seen in later infancy, is yet to be understood. Adults however use a semantic system to make sense of actions even when an action sequence is missing. ~~The use of a neural measure like ERPs provides rich insight into the changes of neural mechanisms underlying action perception during development that may not be detected by behavioral studies.~~

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