Social Neuroscience

ISSN: (Print) (Online) Journal homepage: https://www.tandfonline.com/loi/psns20

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To cite this article: Margaret Addabbo & Chiara Turati (2020) Binding actions and emotions in the infant's brain, Social Neuroscience, 15:4, 470-476, DOI: 10.1080/17470919.2020.1760130

To link to this article: https://doi.org/10.1080/17470919.2020.1760130

SOCIAL NEUROSCIENCE
2020, VOL. 15, NO. 4, 470–476
https://doi.org/10.1080/17470919.2020.1760130

Binding actions and emotions in the infant's brain

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ABSTRACT
The first year represents an exceptional time of development during which important social skills emerge, like action and emotion understanding. However, to date, no study explored the neural underpinnings of infants' ability to bind emotion- to action-related information. To assess this issue, we measured EEG activity while 6-month-old infants observed the same action performed by an actress displaying three different emotional expressions (happiness, anger and neutral). Results have shown that actions embedded in an emotional context (happiness and anger) elicited larger early negativity at parieto-occipital sites compared to a neutral context. This finding suggests that already at 6 months of age, infants use information coming from facial expressions to detect the saliency and relevance of others' actions.

ARTICLE HISTORY
Received 15 May 2019
Revised 8 April 2020
Published online 4 May 2020

KEYWORDS
Action; emotion; infants; ERP

Introduction

During social interactions, infants have to deal with different sources of information. For instance, when they interact with their caregivers, they need to process and combine the information coming from their facial expressions with that originating from their actions. Indeed, emotions and actions are strongly connected. Actions are very often embedded in an emotional context, which reveals not only the internal states of an interactor but also the intention behind his/her actions. Thus, the ability to use the emotional context to detect the relevance of others' actions appears to be fundamental for the development of functional and adequate social interactions. For instance, if the infant observes the caregiver grasping a ball with a happy expression, he might understand that she/he is willing to play and interact with him. Accordingly, actions performed in an emotional context are socioemotionally salient and relevant environmental cues, which might capture infants' attention from very early in life.

Despite the importance of binding the information coming from emotional expressions to intentions during our social encounters, most of the current studies have addressed emotion and action processing separately. Only recently we have witnesses to an increased interest in studying how these two domains interact and affect each other in adult individuals (Conty et al., 2012; Enticott et al., 2012, 2008; Ferri et al., 2013; Grèzes & Dezecache, 2014; Hajcak et al., 2007; Mazzola et al., 2013; Oberman et al., 2007). Intriguingly, it has been shown that the emotional context modulates neural responses to the observation of actions in areas considered part of the so-called "Mirror System" (Ferri et al., 2013). Particularly, during the observation of the same grasping action, happy and angry facial expressions enhanced the activity in the Middle Temporal Gyrus (MTG) and the Superior Temporal Sulcus (STS), while only the angry face modulated neural responses in the Precentral Gyrus (PCG) and the Inferior Frontal Gyrus (IFG) (Ferri et al., 2013). Remarkably, a recent study reported that different social cues, such as emotions, gaze, and gestures, are integrated very early during perceptual processing, 200 ms from stimulus onset (Conty et al., 2012). As such, the link between emotional context and action processing is considered of fundamental importance for our everyday day life and the emergence of adaptive social competences. For instance, when we encounter an angry person, we predict his/her intentions, and we immediately react to potentially harmful situations (Mazzola et al., 2013).

So far, little is known about whether emotional expressions affect the processing of others' actions in infancy and, in particular, infants' neural processing of observed actions. To date, it is established that infants possess sophisticated abilities in both action and emotion processing. Infants start to discriminate between some emotional expressions

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already at birth (Addabbo et al., 2018), and their sensitivity to facial emotional expressions refines during development. By 7 months of age, infants can differentiate at the neural level between different facial expressions (Kobiella et al., 2008; Leppänen et al., 2007). For example, the frontocentral mid-latency Nc ERP component is greater in response to static happy faces compared to angry ones in 7-month-olds (Grossmann et al., 2007; Quadrelli et al., 2019). However, a very recent study has found an opposite result, showing greater Nc and P400 responses to angry facial expressions compared to happy and fearful ones in 5-, 7- and 12-month-olds, and enhanced activation of the N290 to fearful and happy faces compared to angry expressions (Xie et al., 2019). In addition, the Nc is greater in response to both angry and happy facial expressions compared to a neutral one when the presentation is dynamic (Quadrelli et al., 2019).

Concerning action processing, by 6 months of age, infants start to predict, as measured by eye gaze, the goal of simple and familiar actions performed by others (Hunnius & Bekkering, 2010; Kanakogi & Itakura, 2011; Kochukhova & Gredebäck, 2010; Woodward, 1998). Neurophysiological evidence has also shown higher anticipatory ERP activations in response to goal-directed grasping actions compared to non-goal directed actions at 6 months of age (Nyström, 2008). Interestingly, by the end of the first year of life, infants can also benefit from the presence of social contextual information to understand others' intentions. For example, 18-month-olds anticipate a joint or individual action on the basis of the level of engagement (socially engaged or not) with the actor who is performing the action (Fawcett & Gredebäck, 2013). Twelve-month-olds can also use social cues like gaze and emotional expression to anticipate which object an actor is more likely to grasp (Phillips et al., 2002). Lastly, 14-month-olds, but not 10-month-olds, show greater pupil dilation for incongruent face/action pairings and this was taken as evidence of an early understanding of others' action (patting vs. thumping a toy) on the basis of their emotional expressions (happy vs. angry) (Hepach & Westermann, 2013).

In sum, the first year of life is an amazing time of development where babies start to understand others' emotions and to predict others' actions. However, to date, no study has explored how emotional and action information are integrated into the infant's brain. Infants observe in many occasions actions embedded in an emotional context, and binding affective and action-related information might be highly adaptive from very early in life. Here we hypothesize that the emotional context (both positive and negative) could modulate 6-months-olds processing of the same goal-directed action. To assess this issue, we presented 6-month-old infants with a video showing a woman who grasps an object with a different facial expression (happiness, anger and neutral). Crucially, the kinematics of the actions in the three different emotional contexts was kept constant.

Studies in adults have documented ERP components sensitive to body/body parts movements. Specifically, observing hand movements elicits a negative parietal ERP at around 200 ms post-stimulus (N200), which has been related to the activation of fronto-parietal brain regions involved in action processing (Babiloni et al., 2003; Nishitani & Hari, 2000; Wheaton et al., 2001). Further, the view of dynamic body movements elicits an early N190 in occipito-temporal sites, which is sensitive to emotional and motion information (Borhani et al., 2015). In addition, in 8 months-old infants, neurophysiological evidence has shown that the view of biological motion originates early ERPs (200–300 ms) in posterior sites (Hirai & Hiraki, 2005; Reid et al., 2008, 2006), which differentiate between biological vs. scrambled gait (Hirai & Hiraki, 2005), upright vs. inverted body motions (Reid et al., 2006) and possible and impossible movements (Reid et al., 2008). In line with this literature, we expected emotional-related modulations of early ERPs at posterior sites in 6-months-old infants during the observation of the grasping action. Specifically, we predicted enhanced neural responses to actions embedded in an emotional context (happy and angry) compared to a neutral context.

Methods

Participants

The final sample included 21 healthy full-term 6-month-olds (11 females, mean age = 6 months 7 days, range = -185–199 days). An additional 20 infants were also tested, but were not included in the final sample due to fussiness at the beginning of the experiment (not watching the stimuli at all because they started crying, watching away, complaining) (N = 7) and no completion of an adequate number of trials to be considered for data analysis (i.e., 8 trials per condition; N = 8), or eye and body movements that resulted in excessive recording artifacts (N = 5). This high dropout rate is typical in EEG studies with infants (Stets et al., 2012). The protocol was carried out in accordance with the ethical standards of the Declaration of Helsinki (World Medical Association, 1991, pp. 302, 1194) and approved by the Ethical Committee of the University of X. Parents gave their written informed consent.

Stimuli, apparatus, and procedure

Testing took place in an electrically shielded and dimly illuminated room. Infants were seated on the parent's lap approximately 60 cm from a 24-inch screen used for stimulus presentation. A video camera installed above the screen recorded a video of the infant, which was synchronized with stimulus presentation for off-line coding of eye and body movements occurring during each trial. Infants were presented with 3 colored movies showing an actress (face, torso and an arm) performing an action in three different emotional contexts: 1) Happiness: the actress smiles and then grasps a ball, 2) Anger: the actress displays anger and then grasps a ball, 3) Neutral: the actress moves her mouth and then grasps a ball. The total duration of each movie was 2000 ms; in the first 400 ms the actress dynamically expressed one of the three emotional facial expressions. Then, after a further 360 ms, the grasping action started, and the movement lasted for 840 ms. Then the video remained still for further 400 ms (Figure 1). The amount of movement was matched between the dynamic emotions. We extracted the motion information from the facial expression movies using Matlab (Mathworks, Inc., Natick, MA). For two consecutive frames of the recorded movies, the quantity of motion was quantified in every pixel as the sum of the squared differences in the red, green, and blue channels and then summed over all pixels (Schippers et al., 2010). Results show that there is no significant difference between the amount of motion of the angry (M = 20.07; SD = 7.16), happy (M = 19.40; SD = 6.31) and neutral movie (M = 20.94; SD = 8.96) (All *ps* >.542). The kinematic of the actions in the three experimental conditions were identical. To obtain such an identity, we applied a video editing procedure called Blue Screen technique to superimpose on the same trunk different dynamic facial expressions. The dimension of the face from a distance of 60 cm from the screen was 5.75° of visual angle height and 9.5° in width.

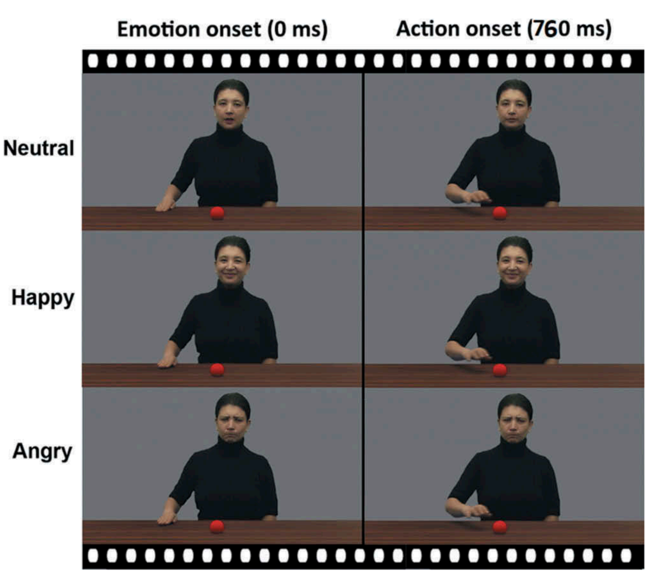

Figure 1. Two example frames taken from the video clips in the neutral, happy and angry conditions.

There was no restriction in the number of trials shown, i.e., they could be played indefinitely until infants got fussy and did not pay attention to the stimuli anymore (i.e., infants looked away for more than five consecutive trials). The three different conditions were presented in a pseudorandomized order by E-prime 2.0 software. Each trial started with a screensaver image (presented in the position where later will appear the face). The screensaver lasted 2000 ms and was dynamic for the first 1500 ms and then static for the remaining 500 ms. Then, one of the three movies was presented to the infant. Stimuli were validated by 15 adults (10 females, mean age = 29.6 years, SD = 3.06) who were asked to judge 1) the depicted expression with a forced-choice task with 4 response categories (happy, angry, neutral, other); 2) the intensity of the expression on a 5 point Likert-scale (from "not intense" to "very intense"). All participants correctly judged the angry, happy and neutral emotional expressions as expressing respectively anger, happiness, and neutrality. Further, no significant difference was found between angry (M = 3.50; SD = 0.90), happy (M = 3.11; SD = 0.66) and neutral (M = 3.02; SD = 1.19) facial expressions intensity ratings (T-test, All ps > .253).

ERP recording and analysis

Continuous scalp EEG was recorded from a 128-channel HydroCel Geodesic Sensor Net (Electrical Geodesic, Eugene, OR) that was connected to a NetAmps 300 amplifier (Electrical Geodesic, Eugene, OR) and referenced online to a single vertex electrode (Cz). Channel impedance was kept at or below 100 KΩ, and signals were sampled at 500 Hz. EEG data were pre-processed off-line using NetStation 4.5 (Electrical Geodesic, Eugene, OR). The EEG signal was segmented in 1000 ms epochs post-action onset, with a baseline period beginning 100 ms before the onsets. Data segments were filtered using a 0.3–30 Hz band-pass filter and baseline corrected using mean voltage during the 100 ms pre-stimulus period. Automated artifact detection was applied to the segmented data to detect individual sensors that showed > 200 µV voltage changes within the segment period. The entire trial was excluded if more than 18 sensors (15%) overall had been rejected. Data were then inspected manually to mark as bad segments containing drift and eye blinks. Of the remaining trials, individual channels containing artifacts were replaced using spherical spline interpolation. For each participant, average waveforms were generated within each experimental condition only if at least 8 artifact-free trials were overall available per condition. Averaged data were then re-referenced to the average reference. The mean number of trials across conditions was 13.6 (min 8-max 21) for the happy condition and 13.1 (min 8-max 24) for the angry condition and 13.3 (min 8-max 23) for the neutral condition.

Inspection of the grand-averaged waveforms in response to the action revealed an early negative ERP component at parietal-occipital sites within the 150–450 time window from action onset. Thus, differences in ERP responses to the action were analyzed over a cluster of parieto-occipital electrodes (52-53-54-59-60-61-65-66-67-70-71 over the left hemisphere and 76-77-78-79-83-84-85-86-90-91-92 over the right hemisphere) (Figure 2).

In order to explore whether infants could discriminate between the three different facial expressions, ERPs elicited in response to facial expressions were also analyzed, showing emotional differentiation in the early posterior N290 and in the mid-latency Nc. Detailed information about this analysis could be found in the Supplementary material, S1.

Results

The ANOVA for mean amplitude with Emotional context (Angry, Happy, Neutral) and Hemisphere (Left, Right) as within subject factors revealed a main effect of Emotional context, $F(2,40) = 6.409$, $p = .004$, $\eta_p2 = .243$. No other effect reached significance (All $ps > .92$). The significant main effect of Emotional context was further explored with planned T-tests (Bonferroni-Holm correction). The mean amplitude of the posterior negativity was larger in response to Happy ($M = -5.69$ µV, $SD = 6.92$) compared to Neutral Expressions ($M = -1.99$ µV, $SD = 5.84$), $t(20) = 2.881$, $p = .018$, $d = .629$. The mean amplitude of this negative deflection was also larger in response to the Angry ($M = -5.66$ µV; $SD = 5.11$) compared to the Neutral Expression ($M = -1.99$ µV, $SD = 5.84$), $t(20) = 3.149$, $p = .005$, $d = .687$. No significative difference was found between Happy ($M = -5.69$ µV, $SD = 6.92$) and Angry ($M = -5.66$ µV; $SD = 5.11$) conditions, $t(20) = 0.031$, $p = .97$, $d = .007$ (Figure 2).

Discussion

The aim of this study was to examine ERPs modulations in 6-month-old infants in response to the same object-directed grasping action performed in three different emotional contexts (Happy, Angry and Neutral). Our results revealed that the affective information conveyed in facial expressions can exert a modulation of ERPs elicited by action observation. Specifically, the modulatory effect of emotion processing occurred at parieto-occipital sites between 150 and 450 ms from action onset and was indexed by a negative deflection that was greater in amplitude during the observation of the same action embedded in an emotional context (both angry and happy) compared to a neutral one. Thus, 6-month-olds infants processed differently an action performed in an emotional context (happy and angry) compared to a neutral one. This result suggests that actions performed in an emotional context might represent salient and relevant sources of information for infants. One may claim that the measured ERP in response to the action onset might reflect the continued response to the facial expression itself (in isolation) rather than to the integration of emotion- and action-related information. However, ERP differential responses to static and dynamic facial expressions in isolation are typically found much earlier (Quadrelli et al., 2019; Xie et al., 2019) than the ERP modulation we have found in response to the grasping action. Indeed, early modulations of the occipito-temporal N290 and of the central Nc in response to facial emotional expressions were also found in the present study, showing early discrimination between happy, angry and neutral facial expressions. In particular, the early N290 was larger in response to Angry compared to Neutral facial expressions, while the opposite pattern of activation was found in the mid-latency Nc. Further, no differences were found in the occipito-parietal electrode site in the 400 ms time window

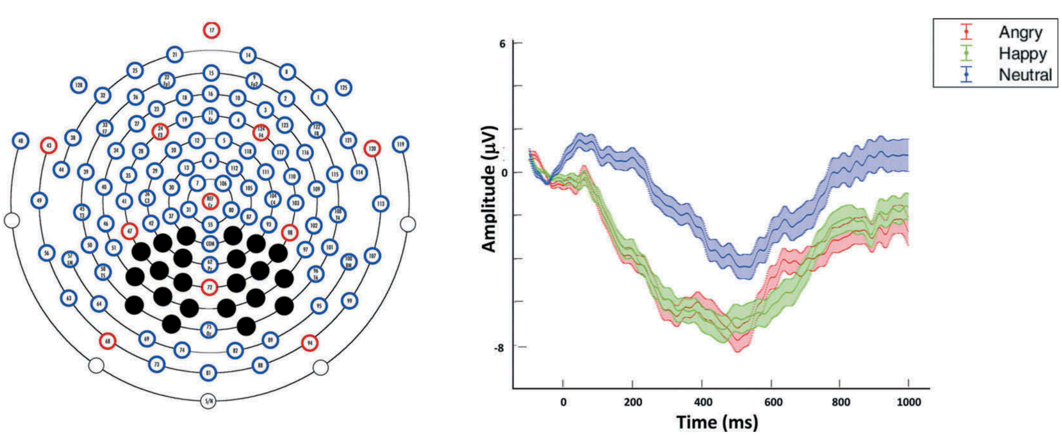

Figure 2. Average waveforms elicited at the onset of the action over the parietal-occipital cluster.

preceding the action onset (see Supplementary material, S1). This result suggests that differential responses to the action didn't reflect a carry-over effect of a preceding divergent activity elicited by facial expressions. Overall, the timing and specificity of the ERP response found in our study strongly suggest that such brain activation was elicited by the reaching action, which was presented in infants' visual field, and that was most likely processed by them within the emotional context. However, future studies might directly address this issue by adding a no-action control condition showing only the emotional expression throughout the 2000 ms video.

To date, most of the current studies have addressed the emergence of infants' ability to process actions and facial expressions in isolation. However, actions are most of the time embedded in an emotional context, and it is fundamental in life to be able to link emotion- to action-related information. Recently, a behavioral study conducted by Hepach and Westermann (2013) has shown that only at the end of the first year of life, infants seem to be able to bind a type of action (i.e., patting or thumping a toy) to a specific facial expression. It appears, then, that the ability to link a type of action to the corresponding emotion emerges only later in development. Infants may need more sophisticated social and cognitive skills, acquired only around the end of the first year of life, to develop this ability. Interestingly, our study shows that the precursors of the ability to bind affective cues to actions might be traced earlier in life. This is in line with previous evidence showing that emotions are extremely salient stimuli that can facilitate infants' perceptual and cognitive processing. For example, by 3 months of age, the processing of novel objects is modulated by emotional expression (Hoehl et al., 2008).

In the present study, we are not able to determine the cortical sources of infants' scalp negative activation. Ferri et al. (2013) reported emotion-related modulations during the observation of actions in brain regions belonging to the action observation circuitry, as the occipital cortex, the STS and frontal motor areas. These brain areas are part of a fronto-parietal network, which is also involved during the execution of an action (Nishitani & Hari, 2000; Rizzolatti et al., 2001). Accordingly, areas involved in action observation processing could have contributed to the differential emotion-related activation found in our study in response to the observation of grasping actions. Future research with infants might explore the effect of emotional context on mu rhythm desynchronization during action observation as a direct measure of sensorimotor cortex modulation (Marshall & Meltzoff, 2011).

Furthermore, the interplay between actions and emotions suggests the existence of anatomical and functional connections between brain regions supporting each of these two domains. Indeed, fMRI studies in adults have found neural connections between emotion- (i.e., limbic system) and motor-related areas through which the emotional context may drive the motor system (Grèzes & Dezecache, 2014). Ferri et al. (2013) suggested that the engagement of the STS might be fundamental to allow the binding of emotion- to action-related information given its connections to both the limbic and the motor system (Carr et al., 2003). The Amygdala (AMG) is also considered a key structure, which directly interfaces with the motor system to prepare adaptive and reactive behaviors (Grèzes & Dezecache, 2014). Here, infants showed at the neural level to process differently an action performed in an emotional compared to a non-emotional context. Remarkably, this differential activation cannot be attributed to low-level features, like motion kinematics, as goal-directed grasps were identical in all the experimental conditions. Further, our results suggest that emotion- and action-related information is linked very early in the infants' brain. Thus, our finding is in line with previous studies with adults showing early integration (200 ms) of different social cues, such as emotion, gaze, and gesture (Conty et al., 2012).

To sum up, in the present study we have shown that emotion- and action-related information are tightly connected already in the first year of life. Investigating how infants integrate and combine information coming from different domains of social cognition is essential to understand how they process more complex situations similar to the ones that they daily encounter during their life. In fact, infants are often engaged in interactions with people who display emotions together with their actions or intention to act. An action performed in an emotional context might acquire for infants a certain relevance among other events in the world. For instance, an action performed in a negative context can be potentially threatening, while an action performed in a positive context can prompt people to engage in social interactions (i.e., play, explore). Thus, emotion information might be a fundamental clue that allows infants, from very early in life, to respond efficiently to relevant behaviors that occur in their environment.

Acknowledgments

We thank the babies who participated in this study, their parents, and Ioana Marchis for assistance with testing. We also thank Lucian Zarnescu for the help in creating the stimuli and special thanks to Carlo Toneatto for his technical support.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This work was supported by the ERC Starting Grant to Chiara Turati [ODMIR 241176].

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