



## Note

# Skin conductance reveals the early development of the unconscious processing of emotions



Elena Nava <sup>a,c,\*</sup>, Daniele Romano <sup>a,c</sup>, Massimo Grassi <sup>b</sup> and Chiara Turati <sup>a,c</sup>

<sup>a</sup> University of Milan-Bicocca, Department of Psychology, Milan, Italy

<sup>b</sup> University of Padua, Department of General Psychology, Padua, Italy

<sup>c</sup> NeuroMI, Milan Centre for Neuroscience, Italy

## ARTICLE INFO

## Article history:

Received 1 March 2016

Reviewed 08 April 2016

Revised 1 June 2016

Accepted 14 July 2016

Action editor Stefan Schweinberger

Published online 22 July 2016

## Keywords:

Emotions

Conscious

Unconscious

Skin conductance

Development

## ABSTRACT

The ability to rapidly distinguish between positive and negative facial expressions of emotions is critical for adaptive social behaviour. Increasing evidence has shown that emotions can be processed even at an unconscious level in adults. Yet, very little is still known about the early ontogeny of the unconscious processing of emotional signals conveyed by faces. Here, we investigated the processing of subliminally presented face emotional stimuli in infants as young as 3–4 months of age and sought to clarify its neural underpinnings by exploring the role of the autonomic nervous system. Using a visual preference paradigm, Experiment 1 determined the visibility threshold for happy and angry faces and established that infants detected both happy and angry faces at 200- but not at 100 msec. By measuring skin conductance response (SCR), Experiment 2 showed that the autonomic nervous system of infants reacted to both subliminally (100 msec) and supraliminally (200 msec) presented face expressions of emotions, and that SCR were higher for angry than happy facial expressions. Results revealed that 3–4 month-old infants respond to positive and negative emotions even at an unconscious level, but also show that angry faces possess an intrinsic alerting characteristics, suggestive of an adaptive meaning of the physiological response. Findings are discussed in terms of subcortical learning of emotions, and the possibility that the amygdala may be involved in such process.

© 2016 Elsevier Ltd. All rights reserved.

## 1. Introduction

Adult human studies have shown that emotional functioning may occur outside conscious awareness. This unconscious

route helps responding efficiently and quickly to the crucial social signals available in the environment (e.g., Dimberg, Thunberg, & Elmehed, 2000; Tamiotto & De Gelder, 2010). This is particularly evident for negative emotions. When presented with extremely brief (i.e., subliminal) fearful and

\* Corresponding author. University of Milan-Bicocca, Department of Psychology, Piazza dell'Ateneo Nuovo 1, 20126 Milan, Italy.

E-mail address: [elena.nava@unimib.it](mailto:elena.nava@unimib.it) (E. Nava).

<http://dx.doi.org/10.1016/j.cortex.2016.07.011>

0010-9452/© 2016 Elsevier Ltd. All rights reserved.

happy facial expressions, followed by a long (i.e., supraliminal) neutral expression, individuals explicitly reported seeing the neutral expressions; however, the fMRI scans revealed that the amygdala responded even to the subliminal portion of the stimuli, demonstrating the processing of emotional stimuli outside conscious awareness (Whalen et al., 1998; for a critical discussion about the topic, see; Pessoa, 2005).

Recently, there has been growing interest – yet still very little evidence – in the early development of the unconscious processing of human faces in infants. Gelskov and Kouider (2010) investigated the duration needed (i.e., the threshold) by 5-, 10-, and 15-month-old infants to discriminate a face from a scrambled face by means of an infant-friendly version of the backward masking paradigm. The face and the scrambled face had durations ranging between 50 and 500 msec, were simultaneously presented on the sides of a screen, and were followed by identical scrambled face-masks. The authors found that 5- and 10-month-old infants did not show any side preference for durations shorter than 100 msec, which could thus be considered below infants' visibility thresholds. In contrast, both age groups looked longer at the target faces than the scrambled faces for durations longer than 150 msec, which were therefore considered above infants' visibility thresholds. This developmental pattern was further confirmed in a study by Kouider et al. (2013), which, based on the visibility thresholds established in a previous paper (Gelskov & Kouider, 2010), demonstrated that infants between 5 and 15 months of age already show a neurophysiological marker of conscious and unconscious processing that resembles those of adults, as observed by the presence of a late nonlinear cortical response measured with event-related potentials.

Recently, two studies investigated whether unconscious processing in infants also extends to facial expression of emotions. Jessen and Grossmann (2015) showed that the electroencephalographic response of 7-month-old infants to subliminally and supraliminally presented stimuli – happy and fearful facial expressions – differed at specific electrode sites. Central electrodes responded differently as a function of the emotion, but not as a function of stimulus duration. In contrast, occipital electrodes had different responses to the two emotions only when emotions were presented supraliminally. These findings suggest that distinct brain processes underlie conscious and unconscious emotion processing early in development.

The above studies had the merit to pave the way for the investigation of the development of unconscious processing of emotions in infants. However, several issues remain unexplored. First, although Gelskov and Kouider (2010) showed that the visibility threshold for faces is 150 msec for infants aged 5- and 10-months, no study yet has assessed whether this is true for emotionally valenced faces. Indeed, Jessen and Grossmann (2015) found different brain processes for stimuli presented at 50–100 msec (unconscious level of processing) and 500 msec (conscious level of processing), but because they did not conduct a behavioural study to estimate the visibility threshold of their stimuli, they could not assess whether ERP responses reflected activity to different suprathreshold stimuli.

Second, the processes underpinning the unconscious processing in infants remain largely unknown. Jessen and Grossmann (2015) found that the unconscious processing of emotions occurs at later latencies (at central electrode sites) compared to the processing of conscious information. Interestingly, the authors suggested that this result could be explained in terms of recruitment of subcortical structures involved in the processing of unconscious information, which cannot be directly observed with ERPs.

Here, we investigated the early development of the response to conscious and unconscious emotionally valenced stimuli by presenting happy and angry faces to 3–4 month-old infants using a behavioural (Experiment 1) and a physiological approach (Experiment 2). Experiment 1 addressed the issue of the early development of visibility thresholds for emotional faces by testing 3–4 month-olds on an adapted version of Gelskov and Kouider (2010) and Jessen and Grossmann (2015) masking paradigm. We hypothesised that infants would detect happy and angry faces at 200- but not at 100 msec. Furthermore, to tap into the early roots of conscious and unconscious processing of emotional information, Experiment 2 used a physiological index – the skin conductance response (SCR) – to measure the activation of the autonomic system to positive and negative emotional facial expressions. We hypothesised that if the autonomic system reacts to both subliminally and supraliminally presented emotional stimuli, we would observe SC activity for both target durations (200 and 100 msec). Furthermore, if negative faces have a privileged access because of their adaptive meaning, we would find higher SCR to angry than happy faces.

Skin conductance is a classical physiological technique to investigate the response of the autonomic system. It tracks the momentary changes in the electrical resistance of the skin and reflects the functioning of the sweat glands controlled by the sympathetic nervous system (Dawson, Schell, & Filion, 2000). It is also a very well suited method to investigate emotional reactions, and correlates with activation of subcortical structures, in particular the amygdala (although it does not directly assess its activity). Neurophysiological studies have shown that fearful and angry facial expressions activate the amygdala, which has connections to both sensory areas and autonomic reflex centres (Davis & Whalen, 2001; Hariri, Tessitore, Mattay, Fera, & Weinberger, 2002). The central nucleus of the amygdala (CeA) projects to areas involved in the activation of the sympathetic autonomic nervous system, which in turn is activated during observation of fearful and angry facial expressions (Davis & Whalen, 2001; LeDoux, Iwata, Cicchetti, & Reis, 1988). Furthermore, lesion studies have shown that the amygdala influences SCR generation and amplitude (Mangina & Beuzeron-Mangina, 1996), and functional imaging studies have shown a correlation between BOLD signal in the amygdala and SC response amplitude (Hariri et al., 2002; Hoffman, Gothard, Schmid, & Logothetis, 2007). Skin conductance represents a non-invasive, suitable and reliable method to be used with young infants (Baker, Shelton, Baibazarova, Hay, & van Goozen, 2013; Ham & Tronick, 2008). 3–4 month-olds are the youngest infants who can be tested using SCR, as the sympathetic system associated with arousal develops during the first ten weeks of

life, that is, testing before 3 months of age would likely lead to unreliable results (Hernes et al., 2002).

## 2. Experiment 1

### 2.1. Material and methods

#### 2.1.1. Participants

Twenty-four 3–4 month-old infants ( $N = 11$  females, age range: 3 month and 6 days to 4 month and 10 days) were included in the final sample. Ten infants were tested but excluded from the final analyses because of technical error ( $N = 4$ ), or failure to look toward at least 3 trials per condition ( $N = 6$ ). Inclusion criteria for final analyses comprised, for each infants, looking for at least 50% of a trial and to a minimum of 3 trials per condition. All infants were born full term (37–41 weeks) and were in the normal range for birthweight. None had neurological impairments. The parents gave informed consent prior to the experiment. The study was approved by the local ethics committee.

#### 2.1.2. Stimuli and procedure

The stimuli consisted of 4 colour photographs of happy and angry female faces taken from the ‘Nim Stim Face Stimulus Set’.<sup>1</sup> The photographs were cropped within an oval shape. All faces were presented in frontal view and were matched for luminance and contrast. The masks were construed by scrambling the pixels of the target faces. Faces and masks were approximately 15 cm in height and 10 cm in width, and presented on a 24-inch monitor from a distance of 65–70 cm from eye level. Faces and masks were presented simultaneously and positioned on the right and left of the screen, at ca. 30 cm from the middle points of their centres.

The infant was seated on the mother's lap and saw a fixation point (i.e., a cross) for 1000 msec, followed by a face target presented together with a comparison stimulus (i.e., a scrambled version of the target) for either 100 or 200 msec (target) (Fig. 1). Target and scrambled comparison were followed by a mask (backward mask) with a duration of 2000 msec minus the duration of the target stimulus. The mask was the scrambled version of a different target face. The target, scrambled comparison and backward mask were repeated for 4 cycles and then followed by a 1000 blank screen. The total duration of a trial was 10 sec, and the total number of trials was 32 (8 trial  $\times$  condition). At the beginning of each trial, there was a brief melody that was used to capture the infants' attention and that was truncated after 5 sec. The target location was selected randomly before each trial with the constrain that the target could not appear more than five times in a row on the same side.

Number of fixations towards the face-target versus scrambled comparison was coded offline frame-by-frame

from video recordings of the sessions, using Virtual Dub, during each trial, from the time the target appeared until the end of the cycles. Trials in which infants did not look at the stimuli for over 50% of the time were excluded from final analysis. On average, we could use ~5 trials per condition (happy conscious: mean = 5.35, SD = 1.23; happy unconscious: mean = 4.90, SD = 1.80; angry conscious: mean = 5.13, SD = 1.60; angry unconscious: mean = 4.90, SD = 1.45).

Two trained coders, blind as to the purpose of the experiment, assessed whether the infant was looking for at least 50% of the trial. Inter-coder reliability was calculated on the coding of 25% of the participants, and agreement was very robust (.97 on Intra-Class Correlation coefficient).

### 2.2. Results

Analysis was run using the Linear Mixed Models procedure as implemented in SPSS 21.0 (SPSS® Chicago, Illinois). For each child, we calculated the number of times s/he looked towards the target stimulus or the scrambled comparison at each trial. The proportion between the target and the comparison was calculated. This value was entered into a Linear Mixed Model, factoring Emotion (i.e., happy and angry) and Duration (i.e., 100 and 200 msec) as fixed effects, and participants as random factor. We found a main effect of Duration [ $F(1, 465) = 37.32$ ,  $p < .001$ ], caused by infants looking more towards 200- than 100 msec stimuli, irrespective of Emotion [ $F(1, 465) = .50$ ,  $p = .48$ ].

To observe whether the infants discriminated the side at which the target actually appeared, we tested, separately for Duration and Emotion, the proportion of fixations to the target and scrambled comparison against 50%, that is, chance. Looking times towards the target were significantly higher than chance for both happy [67.24%,  $t(23) = 4.84$ ,  $p < .001$ , one-sample  $t$ -test] and angry faces [66.25%,  $t(23) = 4.87$ ,  $p < .001$ , Fig. 2], when they were presented at 200 msec. In contrast, when the target was presented for 100 msec, infants did not look more at the target or the comparison image than chance for both emotions [happy:  $t(23) = 1.31$ ,  $p = .20$ ; angry:  $t(23) = .91$ ,  $p = .37$ ].

Results showed that infants were able to detect the face, irrespective of the facial expression of emotion, only when it was presented at 200, but not 100 msec. Because we established that the shortest stimulus was too short to be detected, whereas the longest stimulus was sufficiently long to be detected, we used these two durations to explore, in a further experiment, whether electrodermal activity in infants would respond to both subliminally and supraliminally presented stimuli.

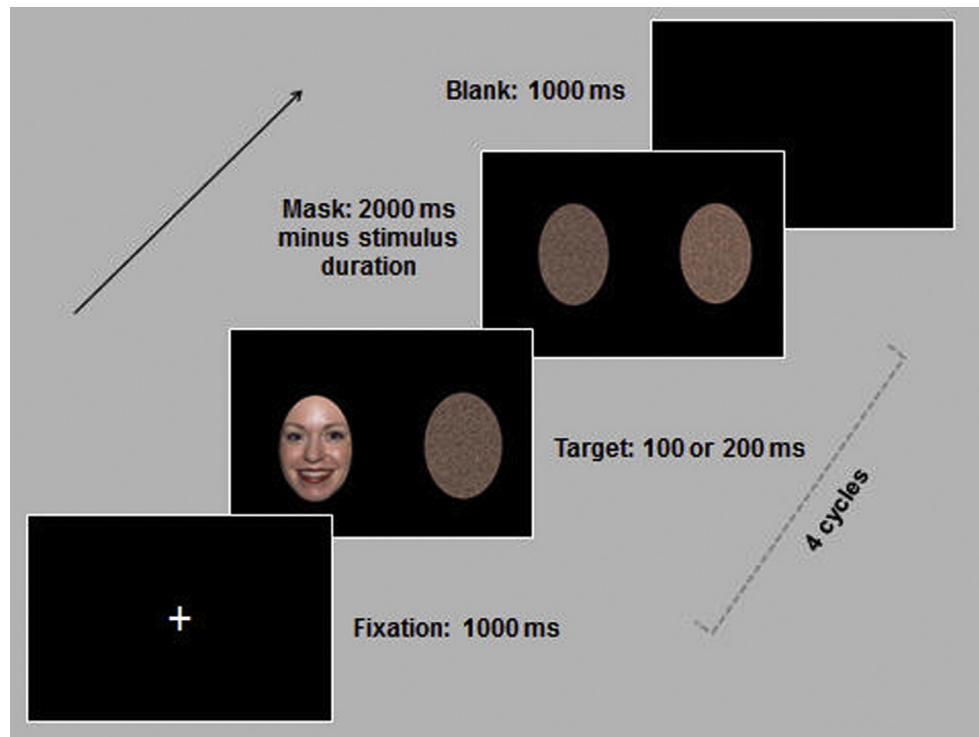
## 3. Experiment 2

### 3.1. Material and methods (extended)

#### 3.1.1. Participants

Twenty-five 3–4 month-old infants ( $N = 11$  females, age range: 3 months and 1 day to 4 months and 10 days), who were not previously recruited for Experiment 1, were included in the final sample. An additional eleven infants were also tested

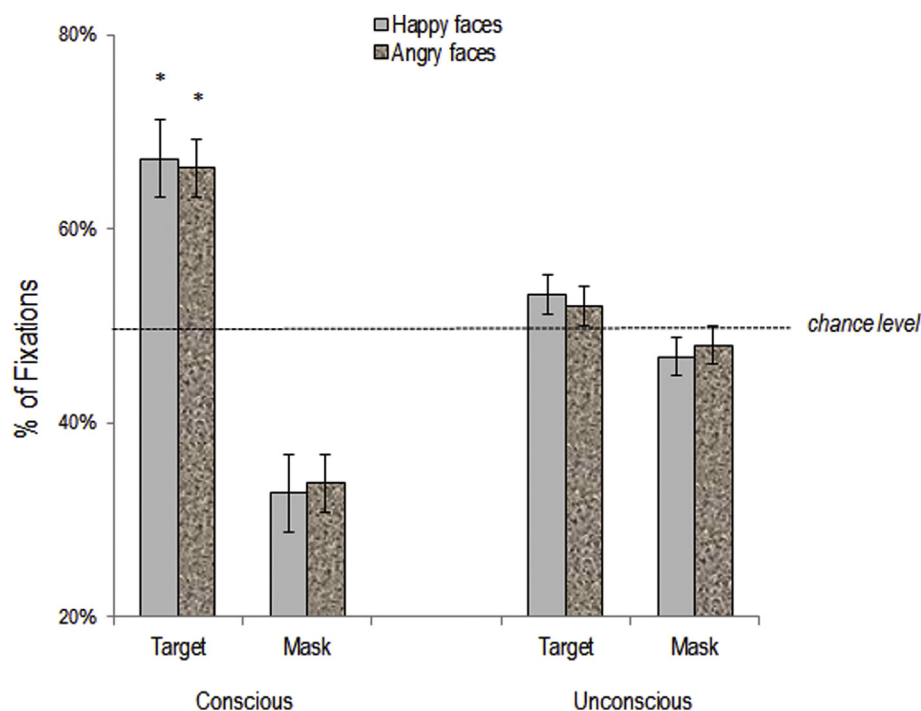
<sup>1</sup> Development of the MacBrain Face Stimulus Set was overseen by Nim Tottenham and supported by the John D. and Catherine T. MacArthur Foundation Research Network on Early Experience and Brain Development. Please contact Nim Tottenham at [tott0006@tc.umn.edu](mailto:tott0006@tc.umn.edu) for more information concerning the stimulus set.



**Fig. 1** – Schematic representation of the paradigm. Infants saw a fixation cross for 1000 msec, followed by the target stimulus, which was presented, on each trial, randomly on either the right or left side and concurrently with the scrambled comparison for either 100 or 200 msec. The backward mask followed the target for 2000 msec. Target and backward mask were presented for 4 times. A blank 1000 msec screen followed the 4 cycles.

but excluded because of fussiness ( $N = 3$ ), failure to look at a minimum of 3 trials per condition ( $N = 5$ ), or technical problems ( $N = 3$ ). Inclusion criteria for final analyses comprised, for

each infants, looking for at least 50% of a trial and to a minimum of 3 trials per condition. All infants were born full-term and did not present neurological impairments. The parents



**Fig. 2** – Results of Experiment 1. Infants were able to detect the face, irrespective of the facial expression of the emotion, only when it was presented at 200-, but not 100 msec. Asterisks indicate values different from chance level.

gave informed consent prior to the experiment. The study was approved by the local ethics committee.

### 3.1.2. Stimuli and procedure

Stimuli and procedure were identical to Experiment 1 with the following differences. First, stimuli were presented at the centre of the screen, so that the SCR could be interpreted exclusively as the consequence of the emotional face presented. Also, because stimuli were presented at the centre of the screen, we limited movement artefacts due to head turning. Second, given that the emotional face stimulus had not to be simultaneously presented with a scrambled comparison (as in Experiment 1), in the current experiment we used neutral faces as backward masks, as in adult studies on this topic (i.e., [Esteves & Öhman, 1993](#); [Whalen et al., 1998](#)). These adult studies have indeed shown that if the stimulus onset asynchrony was sufficiently brief, participants were not aware of the emotionally valenced target face, as assessed by objective forced choice tasks and subjective reports. Furthermore, studies that have compared the effects of facial and non-facial masks (i.e., masks with no face stimuli) have shown that the presence of facial information in the mask is crucial to produce significant masking in face identification ([Costen, Shepherd, Ellis, & Craw, 1994](#); [Loffler, Gordon, Wilkinson, Goren, & Wilson, 2005](#)). Therefore, in this revised version of the backward masking paradigm, infants saw a fixation on a black background for 1000 msec, followed by 4 cycles (i.e., the 200- or 100 msec target and mask presented in rapid succession), of the duration of 2000 msec each and all presented at the centre of the screen (see [Fig. 3](#)). The total

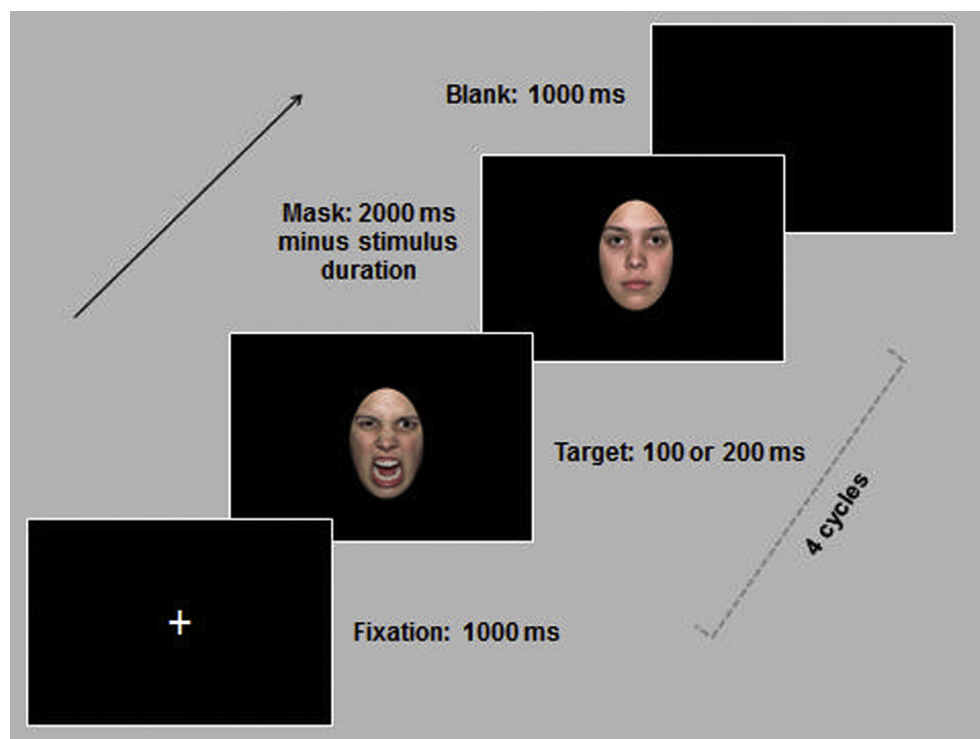
amount of trials in this experiment was the same as in Experiment 1 ( $N = 32$ ). On average, we could use ~6 trials per condition (happy conscious: mean = 6.52, SD = 1.29; happy unconscious: mean = 6.56 SD = 2.00 angry conscious: mean = 6.24 SD = 1.94 angry unconscious: mean = 6.36 SD = 1.91).

Two trained coders assessed whether the infant was looking for at least 50% of the trial, being blind as to the purpose of the experiment. Inter-coder reliability was calculated on the coding of 25% of the participants, and agreement was very robust (.98 on Intra-Class Correlation coefficient).

### 3.1.3. Skin conductance response

SC activity was recorded using an MP150 biosignal amplifier working with the specific acquisition module for skin conductance activity GSR100-C (Biopac Systems, Inc.). The amplifier was connected to the computer through an optical connection. The gain parameter was set at 5  $\mu\text{mho/V}$  and the signal sampled at 100 Hz. The signal was acquired by applying two pre-gelled, self-adhesive, AgAg–Cl electrodes with circular contact areas 1 cm in diameter, directly on the plantar surface of the infant foot (heel and outer edge, see [Ham & Tronick, 2008](#)). Electrodes were secured using adhesive collars.

The analyses of SCR were conducted using AcqKnowledge Software provided by Biopac Systems, which transforms skin conductance level data to provide a SCR by means of a high pass digital filter set at .05 Hz ([Andreassi, 2000](#); [Romano, Pfeiffer, Maravita, & Blanke, 2014](#)). The peak-to-base index was used as indicator of SCR (e.g., the difference between the



**Fig. 3** – Schematic representation of the paradigm used during SC recording. Infants saw a fixation cross for 1000 msec, followed by the target stimulus presented centrally for either 100 or 200 msec. The backward mask followed the target for 2000 msec. Target and backward mask were presented for 4 times. A blank 1000 msec screen followed the 4 cycles.



maximal value recorded in the time window of 8 sec post-stimulus and the baseline calculated on a trial by trial basis, averaging .3 sec of pre-stimulus SC activity, [Rhudy, Bartley, & Williams, 2010](#); [Romano, Gandola, Bottini, & Maravita, 2014](#)).

### 3.2. Results

Analyses were run using the Linear Mixed Models. For each child the peak-to-base measure of each trial was entered into a Linear Mixed Model, factoring Emotion (i.e., happy and angry) and Duration (i.e., 100 and 200 msec) as fixed effects, and participants as random factor.

We did not observe a main effect for Duration [ $F(1, 634) = .05, p = .83$ ], but we did find a main effect of Emotion [ $F(1, 634) = 4.22, p = .04$ ], caused by infants having higher SCR to angry (mean = 1.30, SD = 2.54) in comparison to happy faces (mean = .94, SD = 1.81, see [Fig. 4](#)).

Our results showed that while a SCR was elicited for both subliminal and supraliminal stimuli, angry faces triggered higher responses than happy faces, suggesting that emotions with negative valence are more salient, even if the stimuli were not consciously perceived.

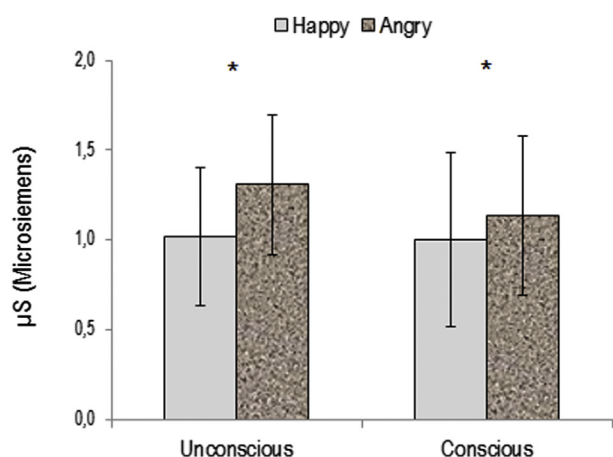
## 4. Discussion

The present study investigated the behavioural response (Experiment 1) and SCR (Experiment 2) for happy and angry facial expressions in 3–4 month-old infants. Infants as early as 3–4 months of age could discriminate a facial expression from a scrambled image at 200 but not 100 msec, suggesting for the first time that even younger infants can detect emotional faces at very short durations. This result was observed regardless of the type of facial expression (Experiment 1). These findings are in line with those observed by [Gelskov and Kouider \(2010\)](#), and further confirmed by [Kouider et al., 2013](#) who found that 5-month-old infants could detect faces in a backward masking paradigm when faces were

presented for durations equal or greater than 150 msec. Here, 3–4 month olds did so at 200 msec, which is plausible, considering that our infants were over 1 month younger than those tested by [Gelskov and Kouider \(2010\)](#). However, it is interesting to note that the authors found a developmental discontinuity, as the visibility threshold did not change between 5 and 10 months of age, and it did change between 10 and 15 months. Combining our results with those of [Gelskov and Kouider \(2010\)](#), it could be claimed that the visibility threshold increases gradually between 3 and 5 months then undergoes an abrupt change between 10- and 15-months of age. However, it is worth noting that, differently from [Gelskov and Kouider \(2010\)](#), we used coloured and not greyscale pictures. Most importantly, our stimuli had an emotional valence, which may trigger a faster visuo-motor response. Overall, the results of Experiment 1 add an important piece of information to the literature concerning face visibility thresholds in young infants, and suggest that emotional stimuli may trigger faster orienting responses leading to lower visibility thresholds compared to simple face presentations.

Moreover, for the first time, we showed that responses to consciously and unconsciously presented facial expressions of emotions can be reliably measured through SC activity in very young infants (Experiment 2). This has important theoretical implications, because it suggests that the autonomic nervous system responds to emotional stimuli before they enter conscious awareness. In particular, we showed that SCR to angry faces are higher compared to happy faces, irrespective of whether the stimulus was presented at a conscious or unconscious level. This finding is in line with the study by [Jessen and Grossmann \(2015\)](#), who found that conscious and unconscious stimuli similarly modulated the activity at central electrode sites, but that the brain responses discriminated between happy and fearful facial expressions. In keeping with this line of evidence, a recent study by [Méndez-Bértolo et al. \(2016\)](#) recorded human intracranial electrophysiological data and found fast amygdala responses only to fearful facial expressions beginning at very short post-stimulus onset latencies. These data support the existence of a subcortical pathway for threat that sends input to the amygdala, and is of critical importance to the understanding of how unconscious stimuli are processed.

However, it should be noted that some studies have shown that only 12-month-old infants present an adult-like sensitivity to angry faces ([Grossman et al., 2007](#)), while in the first months of life a higher sensitivity to happy and fearful faces has been observed, as detected through EEG responses (see [Hoehl, 2014](#) for a review). That is, why might SCR to angry faces ontogenetically precede ERP effects? A possible hypothesis could be that younger infants unconsciously discriminate emotions, as revealed by SCR, but only later in development overtly recognise certain emotional stimuli. It could be speculated that this unparallelled development of overt versus covert discrimination of facial expressions lays in a different development (and recruitment) of subcortical and cortical structures. It has been shown that SCR correlate with activity in subcortical structures – in particular the amygdala – in several fMRI studies, in which adolescent and adult participants were presented with angry faces, both during conscious (e.g., [Hariri et al., 2002, 2003](#)) and unconscious processing of the



**Fig. 4 – Results of Experiment 2. Infants showed a higher arousal for angry than happy faces, irrespective of the duration of the stimulus, that is, they responded to both conscious and unconscious stimuli.**

stimuli, as revealed with priming and backward masking paradigms (e.g., Monk et al., 2008; Morris, Öhman, & Dolan, 1998; Nomura et al., 2004; see also Esteves, Dimberg, & Öhman, 1994; Esteves, Parra, Dimberg, & Öhman, 1994, who combined SCR and backward masking for angry faces). It could be speculated that early in development emotions are “felt” by subcortical regions and are later processed at a more cortical level, which, indeed, could reflect the development of an adult-like awareness of emotion discrimination.

In conclusion, our study shows that infants as young as 3 months of age cannot explicitly detect an emotional expression when it is presented for 100 msec, but they can when the facial expression is presented for 200 msec. Nonetheless, SC activity reveals that emotional facial expressions might be processed even at very short durations and, in particular, that angry faces elicit stronger autonomic responses than happy faces. The fact that infants perceived emotions even when they were explicitly undetectable is important, because it corroborates the view that subcortical nuclei, which are phylogenetically ancient brain structures, precede the emergence of cortical systems involved in conscious perception (Tamietto & De Gelder, 2010). Future studies should investigate whether and how this implicit response might affect and possibly drive infants' behaviour.

## REFERENCES

- Andreassi, J. L. (2000). *Psychophysiology: Human behavior & physiological response*. Hillsdale, NJ, USA: Lawrence Erlbaum Associates.
- Baker, E., Shelton, K. H., Baibazarova, E., Hay, D. F., & van Goozen, S. H. (2013). Low skin conductance activity in infancy predicts aggression in toddlers 2 years later. *Psychological Science*, 24. <http://dx.doi.org/10.1177/0956797612465198>.
- Costen, N. P., Shepherd, J. W., Ellis, H. D., & Craw, I. (1994). Masking of faces by facial and non-facial stimuli. *Visual Cognition*, 1, 227–251.
- Davis, M., & Whalen, P. J. (2001). The amygdala: Vigilance and emotion. *Molecular Psychiatry*, 6, 13–34.
- Dawson, M. E., Schell, A. M., & Filion, D. L. (2000). The electrodermal system. In J. T. Cacioppo, & L. G. Tassinary (Eds.), *Handbook of psychophysiology* (2nd ed., pp. 200–223). Cambridge, UK: Cambridge University Press.
- Dimberg, U., Thunberg, M., & Elmehe, K. (2000). Unconscious facial reactions to emotional facial expressions. *Psychological Science*, 11, 86–89.
- Esteves, F., Dimberg, U., & Öhman, A. (1994). Automatically elicited fear: Conditioned skin conductance responses to masked facial expressions. *Cognition & Emotion*, 8, 393–413.
- Esteves, F., & Öhman, A. (1993). Masking the face: Recognition of emotional facial expressions as a function of the parameters of backward masking. *Scandinavian Journal of Psychology*, 34, 1–18.
- Esteves, F., Parra, C., Dimberg, U., & Öhman, A. (1994). Nonconscious associative learning: Pavlovian conditioning of skin conductance responses to masked fear-relevant facial stimuli. *Psychophysiology*, 31, 375–385.
- Gelskov, S. V., & Kouider, S. (2010). Psychophysical thresholds of face visibility during infancy. *Cognition*, 114, 285–292.
- Grossmann, T., Striano, T., & Friederici, A. D. (2007). Developmental changes in infants' processing of happy and angry facial expressions: A neurobehavioral study. *Brain and Cognition*, 64, 30–41.
- Ham, J., & Tronick, E. (2008). A procedure for the measurement of infant skin conductance and its initial validation using clap induced startle. *Developmental Psychobiology*, 50, 626–631.
- Hariri, A. R., Mattay, V. S., Tessitore, A., Fera, F., & Weinberger, D. R. (2003). Neocortical modulation of the amygdala response to fearful stimuli. *Biological Psychiatry*, 53, 494–501.
- Hariri, A. R., Tessitore, A., Mattay, V. S., Fera, F., & Weinberger, D. R. (2002). The amygdala response to emotional stimuli: A comparison of faces and scenes. *NeuroImage*, 17, 317–323.
- Hernes, K. G., Morkrif, L., Fremming, A., Odegarden, S., Martinsen, O. G., & Storm, H. (2002). Skin conductance changes during the first year of life in full-term infants. *Pediatric Research*, 52, 837–843.
- Hoehl, S. (2014). Emotion processing in infancy. In K. H. Lagattuta (Ed.), *Children and emotion. New insights into developmental affective sciences* (pp. 1–12). Basel: Karger.
- Hoffman, K. L., Gothard, K. M., Schmid, M. C., & Logothetis, N. K. (2007). Facial-expression and gaze-selective responses in the monkey amygdala. *Current Biology*, 17, 766–772.
- Jessen, S., & Grossmann, T. (2015). Neural signatures of conscious and unconscious emotional face processing in human infants. *Cortex*, 64, 260–270.
- Kouider, S., Stahlhut, C., Gelskov, S. V., Barbosa, L. S., Dutat, M., De Gardelle, V., et al. (2013). A neural marker of perceptual consciousness in infants. *Science*, 340, 376–380.
- LeDoux, J. E., Iwata, J., Cicchetti, P., & Reis, D. J. (1988). Different projections of the central amygdaloid nucleus mediate autonomic and behavioral correlates of conditioned fear. *Journal of Neuroscience*, 8, 2517–2529.
- Löffler, G., Gordon, G. E., Wilkinson, F., Goren, D., & Wilson, H. R. (2005). Configural masking of faces: Evidence for high-level interactions in face perception. *Vision Research*, 45, 2287–2297.
- Mangina, C. A., & Beuzeron-Mangina, J. H. (1996). Direct electrical stimulation of specific brain structures and bilateral electrodermal activity. *International Journal of Psychophysiology*, 22, 1–8.
- Méndez-Bértolo, C., Moratti, S., Toledano, R., Lopez-Sosa, F., Martínez-Alvarez, R., Mah, Y. H., et al. (2016). A fast pathway for fear in human amygdala. *Nature Neuroscience*. <http://dx.doi.org/10.1038/nn.4324>.
- Monk, C. S., Telzer, E. H., Mogg, K., Bradley, B. P., Mai, X., Louro, H. M., et al. (2008). Amygdala and ventrolateral prefrontal cortex activation to masked angry faces in children and adolescents with generalized anxiety disorder. *Archives of General Psychiatry*, 65, 568–576.
- Morris, J. S., Öhman, A., & Dolan, R. J. (1998). Conscious and unconscious emotional learning in the human amygdala. *Nature*, 393, 467–470.
- Nomura, M., Ohira, H., Haneda, K., Iidaka, T., Sadato, N., Okada, T., et al. (2004). Functional association of the amygdala and ventral prefrontal cortex during cognitive evaluation of facial expressions primed by masked angry faces: An event-related fMRI study. *NeuroImage*, 21, 352–363.
- Pessoa, L. (2005). To what extent are emotional visual stimuli processed without attention and awareness? *Current Opinion in Neurobiology*, 15, 188–196.
- Rhudy, J. L., Bartley, E. J., & Williams, A. E. (2010). Habituation, sensitization, and emotional valence modulation of pain responses. *Pain*, 148, 320–327.
- Romano, D., Gandola, M., Bottini, G., & Maravita, A. (2014). Arousal responses to noxious stimuli in somatoparaphrenia and anosognosia: Clues to body awareness. *Brain*, 137, 1213–1223.

- Romano, D., Pfeiffer, C., Maravita, A., & Blanke, O. (2014). Illusory self-identification with an avatar reduces arousal responses to painful stimuli. *Behavioural Brain Research*, 261, 275–281.
- Tamietto, M., & De Gelder, B. (2010). Neural bases of the non-conscious perception of emotional signals. *Nature Reviews Neuroscience*, 11, 697–709.
- Whalen, P. J., Rauch, S. L., Etcoff, N. L., McInerney, S. C., Lee, M. B., & Jenike, M. A. (1998). Masked presentations of emotional facial expressions modulate amygdala activity without explicit knowledge. *The Journal of Neuroscience*, 18, 411–418.