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Abstract

Predictive Processing (PP) has been suggested to account for early cognitive development (Köster et al., 2020). In this paper, we extend its application to early social coordination in parent-infant interactions. Interpersonal neural synchrony in parent-child interactions is hypothesized to be a function of the coupling of internal generative models for mutual prediction. By aligning these internal models and reducing prediction errors, social uncertainty is reduced, and interpersonal neural synchrony is enhanced. Support for this hypothesis is provided by assessing neural synchrony during mother-infant interaction.

Keywords: neural synchrony; hyperscanning; predictive processing; parent-child interactions

The acquisition of new cognitive capacities through interacting with and learning from others is arguably the hallmark of the human mind. We propose that this form of learning is facilitated by Predictive Processing (PP). Recent research suggests that the PP framework can account for various learning processes, such as infants' statistical learning, motor, and proprioceptive learning as well as their early prediction of actions and social understanding (Koster et al., 2020). In this paper, we test the contribution of PP beyond the individual to interpersonal processes in the context of early social communication.

What is predictive processing?

The Predictive Processing (PP) framework has become prominent in areas of cognitive neuroscience, as it provides a useful framework for understanding how the brain functions (Clark, 2013). According to the PP account, our brain is not merely passively receiving external input, but instead actively and continuously making predictions about upcoming input and events to then infer cause. Whenever a prediction occurs, two types of inference can be employed: active inference and perceptual inference. Active inference implies that the world is adjusted according to internal models through action. Perceptual inference implies that the internal model is adjusted to new sensory information. The predictions are generated by internal models and updated upon actual sensory input. The generative internal models span every level of the neural hierarchy. They exist at basic levels in sensory and motor regions as well as in networks associated with higher-order processes. The discrepancy between prediction and observation, so called prediction errors, then help the generative models to adapt to the environment and minimize prediction errors in the future. Infants as young as 6 months of age demonstrate heightened activity in the occipital cortex in response to a mismatch between an infant's visual expectation and current sensory input (Emberson et al., 2015).

The mechanism behind these internal generative models is consistent with a Bayesian model of the brain.. Predictions are generated using statistical learning, which includes the neural computation of the probability of events in the environment adjusted by the actual incoming sensory information (Friston, 2010). The statistical regularities of the environment subsequently allow an individual to form probabilistic models of the environment. This approach is designed to maximise model evidence and minimise prediction error resulting in a continuous updating of the internal models.

Predictive processing in social interactions

Even though infants' learning abilities have been mostly studied in isolation, a lot of learning opportunities are actually afforded to infants in social interactions. Learning about the social world from and with other people entails, for example, making better predictions about others' actions. These early interactions then help the infant to resolve social uncertainties and to generate better-adapted models to derive more accurate predictions (Hoehl & Bertenthal, 2021). Precise predictions are critical to social communication – otherwise we would not be able to coordinate as quickly and smoothly as already observed in early social interactions (Sebanz & Knoblich, 2009).

Interestingly, repeatedly learning about the world from others, such as caregivers or siblings, will likely lead to more overlapping mental models and predictions among these individuals. The internal models become coupled to one another (*generalised synchrony*) as communication between caregiver and infant ensues while both try to minimise prediction error. Friston and Frith (2015) suggest, that the more successful these dyads are in aligning predictions and actions, the higher the *generalised synchronization* is expected to be. *Generalised synchrony* is formally defined as the systematic alignment or reciprocity of two dynamical systems. Accordingly, generalised synchronisation means that knowing the state of one system (e.g., neural activity in the brain) enables prediction of the others' state (i.e., another's brain). This definition includes both concurrent states as well as lagged states in the two systems. Overall, the alignment of internal models is suggested to be computationally efficient for communication. Synchronized actions function as an optimization principle, which reduces the cost of processing social information (Koban et al., 2019; Shamay-Tsoory et al., 2009). As interpersonal prediction errors are reduced, the environment, including other people, their actions, intentions, and mental states, can be represented more accurately. This model of social interaction offers a plausible mechanism to explain why we spontaneously and intentionally synchronize during social exchanges. The optimization principle for social understanding is especially important to the infant brain, which is generally shown to be slower in processing even basic sensory stimuli (Emberson et al., 2015).

Interpersonal Neural Synchrony

Research with adults using simultaneous recordings of brain activations from several persons, so-called "hyperscanning", suggests that interactive synchrony can be measured as interpersonal synchronization of oscillatory brain activities (e.g., Czeszumski et al., 2020). Synchronization of neural oscillations is assumed to reflect mutual attunement of behavioral and physiological rhythms (Hasson et al., 2012) that are transmitted interpersonally through the environment by coupling of the sensory system of one person to the motor system of another person. This coupling, which is often referred to as neural mirroring, is associated with brain activity of the inferior frontal gyrus (IFG; Kilner et al., 2007). It is important to note, however, that neural synchrony involves more than mirroring. Neural synchrony facilitates internal predictions about the self and others, and thus optimizes behavior during social interactions, leading to more coordinated social communication (Dai et al., 2018). According to Kayhan and colleagues (under review), it is the coupling of these internal models that explains interpersonal neural synchronisation (INS). According to this view, INS is an index of generalised synchrony as interlocutors' brains entrain to one another. This entrainment occurs at the sensorimotor level, in an attempt to reduce prediction error and facilitate mutual prediction during social communication (Hoehl et al., 2020). For social communication to be successful, mutual predictions are necessary and are facilitated through the coupling of the temporo-parietal junction as well as medial (mPFC) and lateral prefrontal cortex (lPFC) (Hoehl et al., 2020; Koster-Hale & Saxe, 2013). Accordingly, mirroring activity in the IFG cannot result in social coordination by itself (Kilner & Frith, 2008). Lastly, there is alternative perspective for explaining how INS could emerge between two or more people. INS could be an epiphenomenon of common entrainment to behavioral cues and of correspondences between actor and observer (Wass et al., 2020), without further implications for the interaction quality.

INS in parent-child interactions

In contrast to the increasing number of hyperscanning studies in adults (Czeszumski et al., 2020), the neural mechanisms of social exchanges in early child development are still poorly understood as few developmental hyperscanning studies exist to date (Nguyen, Bánki, et al., 2020). The emerging evidence shows that adults and children synchronize their brain activities in interactive contexts that require mutual engagement. Similar to the results in adult dyads, INS in adult-child dyads has been mainly identified in medial and lateral prefrontal as well as temporal brain regions associated with socio-cognitive processes (Gvirts & Perlmutter, 2020; Hoehl et al., 2020; Redcay & Schilbach, 2019). These processes include mutual attention, affect sharing (prefrontal cortex), mutual prediction, mentalizing and shared intentions (temporo-parietal junction), which are generally implicated in social communication. Thus far, high interaction quality, marked by joint attention, infant positive affect and/or turn-taking, has been associated with increased INS (Nguyen, Schleihauf, et al., 2020; Nguyen, Schleihauf, Kayhan, et al., 2021; Piazza et al., 2020), suggesting that INS could be a sensitive biomarker for successful mutual attunement between caregivers and their infants.

Current study

Although there is considerable evidence of neural mirroring during social interactions (Marshall & Meltzoff, 2014), it is an empirical question as to whether there is also neural evidence of predictive processing during parent-child interactions or whether the alignment in brain activation is just an epiphenomenon after all. Accordingly, the goal of this study is to compare whether the neural substrate for early social communication is consistent with (1) the PP framework, (2) the mirroring account or (3) whether INS occurs simply due to entrainment to common stimulation. First, we hypothesize that INS may be a mechanism for facilitating mutual prediction through which interacting partners reduce uncertainty in social interactions (FeldmanHall & Shenhav, 2019). We, therefore, expect INS to emerge in medial and lateral prefrontal regions that are consistently associated mutual prediction (Hoehl et al., 2020). Additionally, we expect greater activation in these cortical regions during multimodal stimulation, such as physical contact (Ciaunica & Fotopoulou, 2017). We hypothesize that multi-modal stimulation reduces uncertainty in mother-infant dyads. A converging measure of prediction error or social uncertainty is respiratory sinus arrythmia [RSA] (Gorka et al., 2013). Specifically low levels of RSA are associated with increased sensitivity to unpredictable threat. We, therefore, included a measure of RSA to test whether prefrontal cortex synchrony was specifically associated with prediction error. Second, mirroring of actions by both people in a dyad would result in activation of mirror system (IFG). As such, INS in bilateral inferior frontal regions would provide neural evidence for the mirroring account. In addition to assessing IFG synchrony, we collected behavioral evidence to test whether affect mirroring during social interaction is related to INS. Lastly, common entrainment to external cues would be evidence of INS emerging during joint watching of the same visual stimuli. We therefore included a joint observation condition to control for this alternative interpretation.

Methods

Sixty-nine mothers and their 4-6-month-old infants participated in three experimental conditions (*Figure 1*). During the experiment, the caregiver and infant were either seated next to one another or the infant sat on the caregiver's lap as both were watching a calm aquarium video on a tablet (distal watching and proximal watching conditions). The videos lasted 90 sec. and depicted fish swimming in a tank. The order of the watching conditions was counterbalanced. Next, mother and infant engaged in a 5 min. free play session without toys or singing while both were seated face-to-face (interactive free play condition).

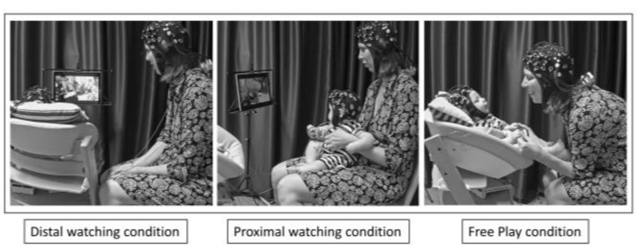

Figure 1: This figure depicts an exemplary mother-infant dyad during the three experimental conditions. We simultaneously measured functional near-infrared spectroscopy and electrocardio-graphy in mother and infant. We also video-recorded the dyad throughout the experiment.

Neural activity for infants and mothers was measured with functional near-infrared spectroscopy (fNIRS). Optodes were located over the inferior frontal gyrus, lateral and medial prefrontal cortex (*Figure 2*). Synchronization in these regions is associated with mutual attention and shared affect, which are critical processes in infants' interactions with their caregivers. The fNIRS time series of mother and infant were both preprocessed using MATLAB toolbox homer2. INS was estimated using Wavelet Transform Coherence (wavelet toolbox), which assesses the relation between two time-series over frequency and time. The coherence for each dyad in each channel combination was averaged over the frequency band of 0.031-0.125 Hz and the whole duration of the condition. We also assessed respiratory sinus arrhythmia (RSA) through electrocardiography (ECG) using a continuous estimation method (Abney et al., 2021). Each dyad was filmed throughout the experiment and the dyads' behavior was micro-coded offline. We assessed affective mirroring in dyads through the co-occurrence of positive facial expressions in mother and infant. Two trained coders coded 25% of randomly chosen videos to assess interrater reliability. Kappa was estimated at .81 and therefore indicated that interrater reliability was high. The duration of affect mirroring was divided by the free play duration and thus proportionate durations of affect mirroring were further considered for statistical analysis.

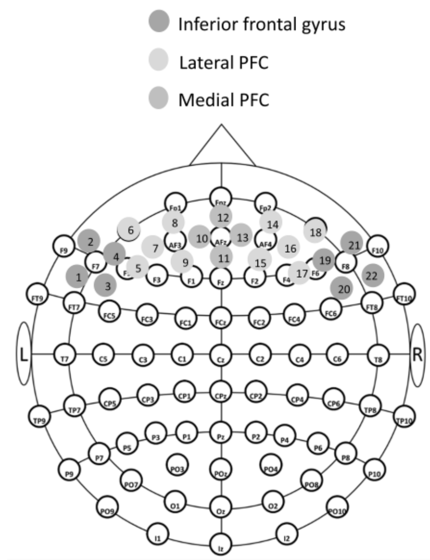

Figure 2: fNIRS channel configuration. Channels 1-4 and 19-22 are located over the inferior frontal gyrus. Channels 5-9 and 14-18 are located over lateral prefrontal areas. Channels 10-13 are located over medial prefrontal areas.

Results

We tested INS (estimated with Wavelet Transform Coherence [WTC]) in oxygenated Hemoglobin concentration changes in the three experimental conditions: non-interactive distal watching condition, non-interactive proximal watching condition, and interactive face-to-face free play condition. The frequency-averaged coherence values between 0.031 and 0.125 Hz were calculated and then further averaged across each condition. Higher coherence values were interpreted as indicators of higher synchrony. WTC was entered as the response variable in the Generalized Linear Mixed Effects (GLME) model, while condition and region of interest were entered as fixed and interaction effects. The model included a random slope for all fixed and interaction effects with random intercepts for each dyad (*N*=69). Results revealed that the fixed effects for condition, $\chi^2(2)=39.91$, *p*<.001, and region, $\chi^2(4)=33.32$, p<.001, as well as their interaction were significant, $\chi^2(8)=25.15$, *p*=.001 (*Figure 3 and Table 1 for descriptive statistics*). Comparisons (using emmeans) across conditions revealed increased neural synchrony during free play and proximal watching relative to distal watching in bilateral lateral prefrontal (lPFC) and medial prefrontal areas (mPFC), *t*(68)=3.10, *p*<.005. The free play condition and proximal watching condition differed in synchronization in the right lPFC and mPFC with higher neural synchronization during free play, *t*(68)=3.06, *p*<.006. Critically, none of the conditions differed in neural synchrony in bilateral inferior frontal gyri (IFG), *p*>.071.

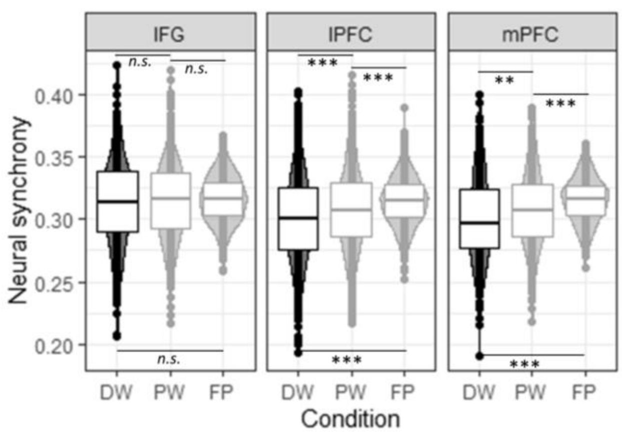

Figure 3: Interpersonal neural synchrony (y axis) between mothers and infants was increased in lateral and medial prefrontal areas (facets) during both free play and proximal joint watching in comparison to the distal watching condition (x axis).

Next, we investigated whether affect mirroring was related to INS during free play between mother and infant. Overall, affect mirroring occurred during 11.18 % of the interactions, but it was not related to INS during free play.

We also assessed whether infants' RSA related to INS during the free play condition. Baseline-corrected RSA (RSA during distal joint watching was subtracted from RSA during free play) was marginally correlated to INS of the dyad, estimate=-0.006, SE=0.003, 95% CI=[-0.012 0.001], $\chi^2(1)=2.980$, p=.084. These results suggest that lower RSA (i.e., higher social uncertainty) was related to higher INS during free play.

Discussion

In the present study, we test whether the neural substrate for social communication in mother-infant dyads is consistent with the PP framework, the mirroring account, or the account on common entrainment. The results of the study revealed that the highest levels of INS emerged when the dyads were mutually engaged in a communicative context during free play. The interactive free play allowed mother and infant to see each other and respond to one another in a timely and contingent manner. In contrast, the dyads did not show INS when they only shared the same visual input and were distanced from one another. Accordingly, our results provide neural evidence against INS emerging due to common entrainment to external cues. Importantly, INS during free play was evidenced in lateral and medial prefrontal areas, but not in inferior frontal areas. Our findings are thus consistent with the notion that mutual engagement in the mother-infant dyad is mediated by dynamic coupling of PFC activity (Nguyen, Schleihauf, et al., 2020; Nguyen, Schleihauf, Kayhan, et al., 2021). The mother-infant dyads also displayed increased INS in the prefrontal cortex when the infant was seated on the mother's lap while watching the videos. One explanation for this effect is that proximity could have facilitated mutual entrainment via micro-adjustments of bodily contact, as well as the perception of heart rhythms and respiration (Wass et al., 2020). As such, these processes could have also contributed to mother-infant neural synchronization.

Prediction vs. mirroring

Social interactions depend on mutual and reciprocal relations (Hoehl & Bertenthal, 2021), processes which involve various neural networks. The results from the current study highlight that social communication in early development relies on the lateral and medial prefrontal cortex (associated with PP), but not in the inferior frontal gyrus (associated with mirroring) where there was no differentiation between free play and passive, distal watching of a video. Moreover, our results align with INS studies in older adult-child dyads, in which evidence converges to show INS in prefrontal areas and not in inferior frontal areas (Nguyen, Schleihauf, et al., 2020; Nguyen, Schleihauf, Kungl, et al., 2021; Piazza et al., 2020; Quiñones-Camacho et al., 2019; Reindl et al., 2018). The cortical localization of INS thus highlights the involvement of brain areas associated with mutual prediction and provides initial evidence against the role of brain areas involved in motor mirroring in INS in mother-infant interactions. Additionally, the results reveal no significant correlation between affect mirroring and INS between mother and infant during free play, thus corroborating the preliminary evidence against the involvement of mirroring in the synchronization of brain activities between mother and infant.

The importance of the PFC in infants' information seeking through action, i.e. active inference, has been emphasized in recent research on the function of the infant PFC (Raz & Saxe, 2020) and is in opposition to accounts in which infants are passive recipients of information. In these latter accounts, it is proposed that humans infer the intentions of others directly through observation of their actions, mediated by the mirror neuron system, part of which is the inferior frontal gyrus (Gallese & Goldman, 1998). According to the PP framework, it has long been argued that action and social understanding, and subsequently social coordination and communication, cannot rely on the inferior frontal gyrus alone to both understand actions and infer intentions (Kilner & Frith, 2008). Instead areas involved in mentalizing and prediction, such as temporo-parietal and prefrontal areas, seem to play a bigger role in successful predictions of actions and intentions as well as the reduction of prediction error (Kilner et al., 2007; Koster-Hale & Saxe, 2013). The PP account, therefore, not only underscores why the PFC was coupled between mother and infant during active mutual engagement, but also implicates the active role of the infant in these interactions.

Additionally, we find preliminary evidence of RSA being related to INS during a free play interaction. Lower levels of RSA have previously been linked with heightened sensitivity towards uncertain, potentially dangerous signals (Gorka et al., 2013). Accordingly, lower levels of RSA could be associated with infant's prediction errors occurring during their social interaction with their mothers. Although these errors may result in inhibiting coordination between mother and infant, it is more likely that infants could actively attempt to repair these instances to improve communication and thus INS. The preliminary results presented in this study provide a hint toward a relation between infants' social uncertainty and neural synchrony, but more definitive evidence must await further evidence.

Co-embodied and multimodal predictions

The PP framework can sometimes appear "neurocentric", yet, in recent years researchers have started to include the body and surrounding environment to make further contributions to the predictive process (Fotopoulou & Tsakiris, 2017; Nave et al., 2020; Seth, 2013). Active inference has been updated to represent a more inclusive account of embodied inference. Employing this inclusive PP account, we suggest that INS was increased during face-to-face interaction as well as physical contact because mother and infant were able to create co-embodied generative models to reduce uncertainty in the situation (Ciaunica et al., 2021). The co-embodiment thesis was initially applied to in utero experiences of mother and fetus during pregnancy. Ciaunica and colleagues (2021) suggest that instead of viewing the fetus as passively "contained" within the mother, pregnancy seems to provide evidence in favor of active and bidirectional co-regulation between two bodies (co-homeostasis). Studies on newborns and infants show, that the unique co-regulatory bond of mother and infant continues out of utero. It is important to note that co-regulation does not need to be reactive, but can occur as a prediction towards changes in the environment (Atzil et al., 2018). Active inferences made through bio-behavioral coordination result in *allostasis* which the infant is not able to establish without the caregiver (Fotopoulou & Tsakiris, 2017).

Consistent with the co-embodiment thesis, our results demonstrate that mother-infant INS increased when mother and infant were physically close to one another (i.e., proximal watching condition). Physical contact could have allowed both mother and infant to draw from more than their own perception, as an increase in arousal or change in body position affects both individuals (Ciaunica et al., 2021). It is similar to how multi-modal perception during face-to-face social interactions helps interlocutors to make mutual predictions about one another. In terms of physical contact, multi-modality emerges with the reduction of distance between interacting partners. In the case of physical contact, the closer two people are to one another, the more heightened their perception of another can be. So instead of relying on visual perception, proximity allows us to draw upon tactile, sensory information of cardio-vascular rhythms, odor information as well as the micro-movements mentioned above.

Still, the results underscore that the mother-infant dyad demonstrates the highest levels of INS when they are able to predict each other during the face-to-face interaction. We suggest, that even though multi-modality in proximity reduced prediction errors to a certain extent, face-to-face interactions must offer an even more reliable sensory stimulation to improve predictions. We suggest that gaze, for example, is a powerful tool to shared and mutual attention (Hoehl & Bertenthal, 2021) and has been shown to facilitate INS (Leong et al., 2017). The predictive role of gaze in mother-infant dyads could therefore be further examined in future studies.

Limitations & future directions

Even though the present study provides preliminary evidence in favor of the neural substrate of mother-infant social communication being consistent with the PP framework, we must remain cautious due to some constraints in the study. The functions of specific brain areas, such as lateral and medial PFC and the IFG are complex and multifaceted, thus caution is warranted, to avoid reverse inference and leaping to conclusions regarding the invoked cognitive processes. The gaze behavior of mother and infant could be measured to computationally model how mother-infant coordination and therefore "predictiveness" in this modality relates to INS in potentially involved brain areas. Another point to consider is that the generation of a common generative model could provide further information on whether the dyad's individual internal models aligned over time. The representations, that are shared by mother and infant could be studied longitudinally. Finally, the spatial resolution of the current study is not as accurate as desired, but could be improved by, for example, MRI co-registration of the channel configuration (see Emberson et al., 2015).

Conclusion

Overall, our study on mother-infant interaction provides evidence for INS during mother-infant free play and when in close physical proximity. These results seem to be consistent with the PP framework, while providing evidence against interpretations of INS based on the accounts of mirroring and common entrainment to external stimuli. Based on the PP framework, we suggest that INS in the prefrontal cortex is related to mutual prediction and attention, as the overall function of INS could be to reduce prediction error. By minimizing uncertainty in social situations, a dyad can create an optimal learning environment for an infant to actively explore what the world has to offer. We suggest that the mother-infant dyad can rely on multi-modal information to improve their mutual predictions during dynamic live exchanges.

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