Introduction

The human brain is an extensive network of finite cortical sources which interact widely during cognitive processing. A coherent and goal-directed response in a rich and complex visual environment requires an integration of these complex brain networks. The major challenge for these networks is their limited capacity to parallelly process a large amount of information and detect vital cues in such a multifarious world. To cope with these limitations, there exist attentional selection mechanisms which guide perceptual processing toward salient/relevant information and resolve competing choices. This filtering plays an important role in day-to-day visual cognition in the natural visual environment where objects are embedded in a complex visual context and often associated with a specific valence. The quality of our daily life environment is greatly dependent upon what to perceive and how fast and accurately we perceive our targets in such a complicated and emotionally charged world. Therefore, our daily visual performance is majorly impacted by the parallel perceptual processing of contextual associations as well as the valence of the visual stimuli.

According to the previous literature, a familiar or congruent object-context association (e.g. spoon in a cup of tea on a table) in a scene can enhance the visual performance whereas an unfamiliar or an incongruent object-context association (a toothbrush instead of the spoon in a cup of tea on a table) could often lead to performance reduction in object identification/categorization tasks although "out of context objects" are better remembered or easily detected (Bar, 2004; Bar and Ullman, 1996; Ganis and Kutas, 2003; Mudrik et al., 2011; Ohman et al., 2001; Rémy et al., 2014; Simpson et al., 2000). Similarly, in visual search tasks where a unique target must be found among distractors, the detection times were faster when the target had some emotional value, such as an angry or happy face among neutral faces or a snake or spider among flowers (Eastwood et al., 2001; Fox, 2002; Ohman et al., 2001). The studies where they have considered both contextual and affective influence during visual perception report modulation of the spatial

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ABSTRACT

Object-context associations and valence are two unavoidable stimulus characteristics when it comes to the processing of natural visual scenes. In line with our previous studies exploring the parallel processing of context-congruity and valence, in the current study, we investigated the valence-specific differences in functional connectivity between congruent-incongruent picture pairs during binocular rivalry using high-density EEG. The functional connectivity measure was calculated using sLORETA during the perceptual dominance of congruent and incongruent stimuli in a time window of 400 ms before the response and compared within and between positive, negative, and neutral valence categories (84 Brodmann’s areas across 7 frequency bands) using t-tests. A significant difference in functional connectivity between congruent-incongruent picture pairs was seen only when associated with negative valence and a maximum number of area pairs showed differences in lower alpha 1 (7.1 – 9 Hz), upper alpha (11.1 – 13 Hz), and beta (13.1 – 30 Hz) frequency bands. The functional connectivity was significantly lower during incongruent perception between the area pairs which process mainly emotion, attention, memory, and semantic relations compared to their corresponding congruent stimuli. Similarly, negative incongruent percepts were found to have significantly lower connectivity between areas processing attention, emotion, and incongruence in the lower alpha 2 (9.1 – 11 Hz) band when compared to positive incongruent percepts. Together, these results suggest that the perception of negative incongruence is associated with lower functional connectivity and this could be a possible reason for the increased error rates when faced with incongruity and negative affect during visual tasks.

Research paper

Altered functional connectivity: A possible reason for reduced performance during visual cognition involving scene incongruence and negative affect

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frequency content of object representations getting influenced by both factors (Caplette et al., 2014), modulation of the weighting of sensory information during predictions regarding what object to find in a particular context by affective content (Caplette et al., 2020), and the role of left medial orbitofrontal cortex in processing both affective value and object-context associativity (Shenhab et al., 2013).

Taking inspiration from such studies, we wanted to explore differential perceptual processing of scene congruency and incongruency separately for each valence category. Since affective and associative (object-context) processes are crucial during perception, it is important to understand whether there is any perceptual bias towards incongruency and if so is it the same across three different valence categories and what are the cortical areas/networks involved.

To unveil this, we conducted a series of experiments where we used an intermittent binocular rivalry (BR) (Pitts and Britz, 2011) to measure the perceptual bias. BR occurs when two different eyes are presented with two different stimuli i.e., one to each eye, and the observer perceives the competing stimuli alternatively instead of a single 3D percept. During BR, at any given point in time, the brain is presented with two competing stimuli, but the brain prefers one over the other. This perceptual dominance is determined by the strength of the stimuli i.e. the bottom-up influence of the physical features of the stimuli as well as by the top-down attentional control, that is, what the brain wants to see. Hence, the stimulus which has maximum predominance during rivalry is considered to have preferential access to consciousness due to its physical or motivational relevance (Tong, 2001; Tong et al., 2006). For our investigations, we presented congruent visual stimuli with a specific valence (an image of a spoon in a cup of tea was considered as congruent and positive) to one eye and its corresponding incongruent stimuli with the same valence (a toothbrush instead of the spoon in a cup of tea was considered as incongruent but still positive) to the other eye. The primary investigation measured the perceptual bias by calculating the dominance duration of congruent and incongruent stimuli within each valence category. The results revealed a perceptual bias towards incongruence when associated with negative and neutral valence but not with positive suggesting a possible valence-congruence interaction during visual perception (Zacharia et al., 2020a). In the next study, the influence of the prestimulus brain state on the perceptual bias of context congruity was investigated and specific pre-stimulus microstates were found to precede the perception of scene incongruency specific to valence indicating that in addition to stimulus attributes, the pre-stimulus intrinsic brain activity could be an important determinant during visual perception (Zacharia et al., 2020b).

Subsequently, we explored the differences in neural source generators between congruent and incongruent contextual associations during their perceptual dominance in BR within each valence category. Various frontal regions were found to have higher activity for incongruent associations specific to valence providing further evidence for the sensitivity of the frontal lobe to both scene congruity and valence (Zacharia et al., 2021) during visual perception. In sequence with these studies, the current study was designed to explore the differences in functional connectivity during the perceptual processing of congruent and incongruent associations within each valence category and further between valence categories.

Although several brain regions have been known to participate in visual scene perception (Aminof et al., 2007; Faivre et al., 2019; Goh, 2004; Mechelli et al., 2004; Mudrik et al., 2010; Rémy et al., 2014), a coherent framework for summarizing the overall architecture of the human scene processing system remains an open question. According to the literature, scene processing is fundamentally divided into two collaborative but distinct scene-processing networks connecting vision and memory (Baldassano et al., 2016). Another set of studies that are focused more on how exactly congruency benefits scene perception through schema activation reports the medial temporal lobe (MTL) and medial prefrontal cortex (mPFC) as the key brain regions which mediate encoding, consolidation, and retrieval of information as a function of its congruency with existing information represented in neocortex and proposed a framework, “Schema-Linked Interactions between Medial prefrontal and Medial temporal regions” (SLIMM), connecting schema, memory, and novelty. According to SLIMM, the mPFC is important for making online predictions enabled by schemas, whereas the MTL is important for detecting the type of novelty associated with an incongruent schema (Kesteren et al., 2010; van Kesteren et al., 2012, 2013).

Recent years have seen a tremendous increase in the use of electroencephalographic techniques (EEG) to measure the neural signature of various cognitive and affective processes. The limited electrophysiological literature (using ERP) regarding the processing of congruent and incongruent stimuli indicates that the earliest difference between the two can be seen around 300 ms and this reflects the analysis of semantic congruency (Mudrik et al., 2010). Similarly, the processing of emotional stimuli involves modulations through various EEG frequencies. Neural activity in the theta range has been reported in the amygdala in response to emotionally arousing stimuli (Pare, 2003). Delta oscillations have been linked with the activity of motivational systems and participate in salience detection (Koyanov, 2007). Alpha frequency is known to show an anterior asymmetry when there is a change in an individual’s affective state (Davidson, 1998; Dimberg and Pettersson, 2000). Another study that has explored beta modulation by facial expressions of emotions, revealed a significant effect only for the angry face (increased beta) (Guntekin and Basar, 2007). Furthermore, the gamma band is also found to be sensitive to emotional stimuli. Similar to theta rhythm, gamma rhythm is also related to the arousal level of the stimuli (Keil et al., 2001).

High-density EEG has been widely used for the assessment of functional connectivity (Hassan et al., 2014; Michel and Brunet, 2019). This analysis identifies electrodes/brain regions that have correlated activity in terms of frequency, phase, or amplitude. Connectivity analysis does not determine the specific direction of information flow in the brain network; instead, it shows that these electrodes/regions have similar signal content and therefore are most likely connected at the functional level. Coherence between signals of sensors covering different scalp areas is commonly taken as a measure of functional coupling. However, this approach provides vague information on the actual cortical areas involved, owing to the complex relationship between the active brain areas and the sensor recordings (Grasman et al., 2004; Schoffelen and Gross, 2009). Hence, for the current investigation, the connectivity analysis was performed in the source space i.e. brain sources reconstructed from scalp signals (source connectivity) where the underlying source activity was used to determine the strength of the connectivity (Astolfi et al., 2004; David et al., 2003; Supp et al., 2007). To the best of our knowledge, no other study has commented upon the networks involved in congruency processing using EEG functional connectivity analysis although there are reports of higher activity in the 30–50 Hz band over right anterior and posterior temporal sites during the processing of pleasant pictures (Müller et al., 1999). Further, viewing highly arousing images led to a significant enhancement of EEG coherence between prefrontal and posterior electrodes in both cerebral hemispheres seen for the beta band (Miskovic and Schmidt, 2010). Both these studies were conducted using 128-channel EEG data.

Similar to our prior investigations, in the current study also, the functional connectivity differences between congruent and incongruent object-context associations within each valence category were assessed during their perceptual dominance in an intermittent BR task. High-density 128-channel EEG was recorded throughout the task and source connectivity (in beta band) was calculated in a time window of 400 ms (mean reaction time) before response execution across 7 frequencies and compared between congruent and incongruent percepts within each valence category. We hypothesized that similar to the previous studies, there would be a significant difference in the functional connectivity between the congruent and incongruent object-context associations across 7 frequency bands and this differential connectivity would be different for distinct valence categories and also significant differences in connectivity would be there between valence categories.
Experimental procedures

Participants

Sixty healthy volunteers (Mean ± SD: Males-n = 28 [27.37 ± 2.88 yrs of age]; Females-n = 32 [26.30 ± 3.47 yrs of age]) of either gender participated in the study. All participants were right-handed as assessed by the Edinburgh Handedness Inventory with normal or corrected-to-normal vision and without any psychiatric or neurological illness history. Out of 60 subjects that participated in the experiment, 40 (Mean ± SD: 26.78 ± 3.52) were right-eye dominant and 20 (Mean ± SD: 26.65 ± 2.88) were left-eye dominant as assessed by a hole in a card test (Shneor and Hochstein, 2006). Before the start of the experiment, written informed consent was obtained from the participants with an option to discontinue anytime if they had any inconvenience during the experiment. The work has been carried out following the Institute Ethics Committee guidelines (Ref No. IESC/T-466).

Stimuli

Congruent – incongruent picture pairs were created and validated for the experiment. To create the picture pairs, pictures depicting real-life day-to-day actions with a specific valence were downloaded from free internet sources and these served as the congruent pictures. Further, to create the corresponding incongruent picture, one object from the original congruent picture was replaced by another unrelated object using Adobe Photoshop software (Fig. 1). Special care was taken to avoid any change in the valence aroused by the original congruent stimuli while replacing it with another unrelated object. The created congruent-incongruent pairs were then validated by taking ratings for valence and congruency, while the reaction time was recorded.

Based on a high rating score and low reaction time for both congruency and valence ratings, 18 congruent–incongruent picture pairs i.e. 6 pairs in each valence category were selected for the BR experiment. A significant demarcation was seen in the valence score between the selected negative, neutral, and positive pictures (Mean ± SD: Negative=-1.64 ± 0.36; Neutral=-5.62 ± 0.34; Positive=7.68 ± 0.04; \( p < 0.0001 \); One-way analysis of variance followed by Bonferroni’s multiple comparison test). Similarly, there was a significant difference in the congruency score of the selected congruent and incongruent pictures (Mean ± SD: congruent=1.39 ± 0.33; incongruent=7.78 ± 0.35; \( p < 0.0001 \); Mann Whitney U test). There was not a significant difference in the congruency scores of congruent pictures between positive, negative, and neutral valence categories (Mean ± SD: Positive=1.22 ± 0.14; Negative=1.367 ± 0.09; Neutral=1.22 ± 0.093; One-way analysis of variance followed by Bonferroni’s multiple comparison test, \( p = 0.06 \)). Similarly, no significant difference was found in the congruency scores of incongruent pictures between positive, negative, and neutral valence categories (Mean ± SD: Positive=7.59 ± 0.39; Negative=7.88 ± 0.23; Neutral=7.923 ± 0.31; One-way analysis of variance followed by Bonferroni’s multiple comparison test, \( p = 0.186 \)). Further, within a congruent–incongruent picture pair, no statistically significant difference was found for valence score, valence rating reaction time, and congruency rating reaction time. The congruency rating score was significantly different between congruent and incongruent stimuli (Table 1). The details regarding the standardization process can be found in (Zacharia et al., 2020a).

Binocular rivalry paradigm

The phenomenon of binocular rivalry is an ancient concept that dates back to 1760. It is used mainly for studying consciousness as well as factors affecting visual perception and hence, is an excellent means to assess perceptual bias. An intermittent BR task was used for the study, in which stimulus presentation alternated with blank intervals (Pitts and Britz, 2011). Binocular rivalry occurs when two incompatible images are presented simultaneously, but separately to each eye. The observer’s perception switches back and forth between the two stimuli that are competing for perceptual dominance (Blake, 2001; Leopold and Logothetis, 1999). In the present study, using a mirror stereoscope, the emotional congruent stimulus was presented to one eye and the other to the other eye.

Table 1

| Congruent | Incongruent |
|-----------|-------------|
| Neutral (Mean ± SD) | |
| Valence score | 7.13 ± 0.15 |
| Valence RT (ms) | 2344 ± 121.2 |
| Congruency score | 1.367 ± 0.09 |
| Congruency RT (ms) | 2387 ± 131 |
| Positive (Mean ± SD) | |
| Valence score | 7.46 ± 0.23 |
| Valence RT (ms) | 2320 ± 134.4 |
| Congruency score | 1.22 ± 0.09 |
| Congruency RT (ms) | 2286 ± 149.4 |

Fig. 1. Stimuli. Examples of picture pairs: A) A butterfly on a flower was considered positive and congruent. B) The flower was replaced by ice cream to make the corresponding incongruent picture which is conflicting with the context but maintained positive. C) Water coming out of a tap was considered neutral and congruent. D) The tap was replaced with a hammer which altered the object context relationship but valence remained neutral. E) A picture of a bleeding nose served as a negative congruent stimulus and F) Placing a worm instead of blood made the picture incongruent without modifying the valence.
corresponding emotional incongruent stimulus was presented to the other eye, creating a competition between the two. The task began with a continuous display of a pair of pictures on the computer screen for 1 min to make sure that the participants were able to appreciate the difference between congruent and incongruent pictures and also to ensure proper superimposition. Once the subjects were familiarized with the picture pair, the pair was presented for 600 ms followed by 600 ms of a blank screen. These 1200 ms constituted one trial and a given pair of pictures was presented for 50 such trials in sequence. Participants were instructed to report a particular percept during each trial by a specific key press i.e., to press key 1 for congruent, key 2 for incongruent, and key 3 for piecemeal rivalry (mix of both the pictures) (Fig. 2A). The task included a random presentation of 3 blocks. Each block consisted of 6 pairs of pictures with one specific valence i.e., positive, negative, or neutral and each pair was repeated 50 times which provided a total of 900 trials (3 blocks X 6 pairs X 50 trials). For half of the trials, the congruent pictures were presented to the right eye and for the other half, they were presented to the left eye (Zacharia et al., 2020a).

**EEG data acquisition**

EEG signal was acquired throughout the task with a 128-electrode HydroCel Geodesic Sensor Net system (Philips Neuro Electrical Geodesics, Inc (EGI)) at a sampling rate of 1000 Hz with 0.03–100 Hz bandpass filter. Participants were seated in a comfortable chair in an acoustically attenuated and electrically shielded room. The recording was done with a common vertex (Cz) as the recording reference, and impedance was kept below 50 kΩ as per the manufacturer’s guidelines.

![Fig. 2. Experimental design and segmentation strategy.](image-url)

A) **Stimuli**

- Congruent
- Incongruent
- Piecemeal (mix of both)

Response:
- Congruent: Press 1
- Incongruent: Press 2
- Piecemeal (mix of both): Press 3

50 trials for 1 pair

B) **Stimuli**

- Stimulus onset
- Response

**Stimulus on**

- Stimulus
- ISI
- Stimulus
- ISI

Stimulus – stimulus
ISI – inter stimulus interval
Response

**Fig. 2.** Experimental design and segmentation strategy. Figure showing A) the intermittent BR task design and B) the segmentation strategy used for the data analysis.
**EEG data pre-processing**

The EEG data were pre-processed offline using Net Station and EEGLAB software. The data was band pass filtered into 1–90 Hz and then segmented backward from the response tag to comment upon the difference in neural processing once the perceptual processing is complete. The segment length was calculated based on the mean reaction time. The mean reaction time (averaged across trials and subjects) was calculated for congruent and incongruent percepts separately within each valence category. No significant difference was seen between the mean reaction time of congruent and incongruent percepts within any of the valence categories and also between valence categories (Zacharia et al., 2020a). Therefore, the mean reaction time was pooled across percepts and valence categories which provided us with a time window of 400 ms before the response onset (Resp-400 ms) for analysis (Fig. 2B). Subsequently, the data were visually inspected for artifacts, and channels showing noise were interpolated by the spline interpolation method. Data were then exported to the EEGLAB toolbox operating in the MATLAB (MathWorks, Natick, MA) environment. Further, the segments in which subjects perceived congruent and incongruent stimuli were identified and separated using a custom-made MATLAB script for each valence category. For the analysis, any trial with a reaction time of less than 150 ms was excluded considering that as an anticipatory response (Dane and Erurumluoglu, 2003). Using Independent Component Analysis (ICA - runica algorithm), ocular, ECG, and power line noises were removed. Further, data were down-sampled to 500 Hz and re-referenced to the common average. The number of congruent and incongruent segments (per subject; Mean ± SD) analyzed were 65.7 ± 10.4 and 67.9 ± 12.8; 54.5 ± 13.2 and 72.8 ± 8.3; 55.4 ± 15 and 90.6 ± 11.6 in positive, negative, and neutral categories respectively.

**Source connectivity analysis**

The current study was performed to understand the difference in connectivity between congruent and incongruent scenes within each valence category. As mentioned in the introduction, the functional connectivity/coherence analysis identifies electrodes/brain regions that have correlated activity in terms of frequency, phase, and/or amplitude. Coherence analysis does not determine the specific direction of information flow in the brain network, instead, it shows that these electrodes/regions have similar signal content and therefore are most likely connected. Thus, coherence across a network means that a specific population of neurons is active at the same time or in a time-related fashion with certain other neuronal populations. If the signals measured from two electrodes or regions are identical then they have a coherence value of 1; depending on how dissimilar they are, the coherence value will approach 0. Coherence between signals of sensors covering different scalp areas is commonly taken as a measure of functional coupling. However, this approach provides vague information on the actual cortical areas involved, owing to the complex relationship between the active brain areas and the sensor recordings. Hence, for the current investigation, the coherence analysis was performed in the source space (source coherence) where the amplitude of the current source density of the underlying dipole was used to determine the strength of the connectivity. The analysis was performed using standardized low-resolution brain electromagnetic tomography (sLORETA) (Pascual-Marqui, 2007). The first step of the analysis was to define a specific Region Of Interest (ROI). The algorithm calculates the current source density at each of the defined ROI across predefined frequencies. For the current study, an 84-ROI file was created using 42 distinct Brodmann areas (BAs) for the left and right hemispheres (supplementary data Table 1). Each ROI consisted of a single voxel i.e. the one that was closest to the center of mass of the ROI. This was the method of choice for two reasons: (1) the single centroid voxel is an excellent representative of the ROI; (2) if the ROI is defined as large (all voxels specified by the ROI), then the average sLORETA activity spanning a large volume might not be very meaningful. In the next step, the covariance of the source signals between the defined area pairs i.e. 84 * 84 BAs across various frequencies between conditions was compared. For the analysis, the frequency band division was estimated based on the Individual Alpha Frequency (IAF) calculated (Doppelmayr et al., 1998; Klimesch et al., 1999) on an adult sample of 180 participants and used the average IAF of that sample. The bands were divided as follows: 1. Delta - 1–4 Hz; 2. Theta - 4.1–7 Hz; 3. Lower alpha; 1.7–7.1 Hz; 4. Lower alpha 2–9.1–11 Hz; 5. Upper alpha - 11.1–13 Hz; 6. Beta - 13.1–30 Hz and 7. Gamma - 30.1–90 Hz.

Connectivity was computed using lagged linear connectivity, which is related to linear similarity i.e., a properly corrected standardized covariance. These measures of connectivity contain only causal-physiological connectivity information. Statistical comparisons were made using independent t-statistics with Statistical non-Parametric Mapping (SnPM) which gives a critical probability threshold for the actually observed t-values with correction for multiple comparisons across all voxels. For each SnPM randomization test, a total of 5000 permutations were used to determine the significance (Nichols & Holmes, 2002). Intracranial generators showing statistically significant changes in functional connectivity were plotted as connecting lines between sources. Plotting was done in the sLORETA connectivity viewer.

**Results**

**Predominance ratio and reaction time**

Predominance ratio is considered the primary index of dominance/perceptual bias during BR. The predominance ratio was calculated using Levelt’s approach i.e. predominance ratio = (D (Congruent) − D (Incongruent))/(D (Congruent) + D (Incongruent)) where D is the dominance duration of the percept averaged across picture pairs (Levelt, 1965). When the relative dominance was assessed, a significant predominance was observed for incongruent precepts in the neutral and negative valence categories but not in the positive block (Mean ± SD: neutral = −0.08 ± 0.12; p < 0.0001; negative = −0.12 ± 0.1; p < 0.0001; positive = −0.028 ± 0.14; p = 0.059; Wilcoxon signed-rank test) although no significant difference was found in the mean reaction time between congruent and incongruent stimuli in any of the valence categories (Mean ± SD: Positive-Con=436.31 ± 130.64; Incon=439.9 ± 125.97; p = 0.85; Negative-Con=443.04 ± 125.31; Incon=441.65 ± 121.09; p = 0.93; Neutral-Con=437.77 ± 137.04; Incon=454.78 ± 219.72; p = 0.88) and also between valence categories (Con-p = 0.86; Incon-p = 0.97). For more details refer (Zacharia et al., 2020a).

**Source connectivity analysis**

Primarily the source connectivity was compared between congruent and incongruent conditions within each valence category separately. Within a category, voxel by voxel independent t statistics was applied between congruent and incongruent conditions with SnPM. SnPM uses a nonparametric permutation/randomization procedure (i.e., based on the Fisher’s permutation method, with the threshold set at the 5% probability level), comparing the mean source connectivity (based on mean source power in each voxel/ROI) between each area pairs (84 *84) and the distribution in the permuted values. For the present study sLORETA used 5000 data randomizations to determine the critical probability threshold values for the actually observed t-test values with correction for multiple comparisons across all voxels and all frequencies, without the need to rely on gausianity. The SnPM allows one to calculate a threshold t-value at a given p-value above which the results are considered to be significantly different. By evaluating the empirical probability distribution of the “maximal statistics” in the null hypothesis, permutation and randomization tests have been demonstrated to be effective in controlling the Type I error in neuroimaging studies (Nichols et al., 2020).
and Holmes, 2002). In the Resp-400 ms time window, when the source connectivity was compared between congruent and incongruent conditions, the threshold t values at p = 0.05 were 3.872, 4.42, and 3.38 for negative, positive, and neutral categories respectively. In positive and neutral categories, we didn’t find any area pairs which had an original t value above the critical threshold calculated using SnPM implying there was no significant difference in source connectivity. In the negative category, the connectivity was found to be significantly different in such a way that incongruent percepts had significantly lower connectivity than congruent percepts for 15 pairs in theta, 68 pairs in LA 1, 5 pairs in LA 2, 34 pairs in UA, and 39 pairs in beta frequency bands (supplementary data Table 2) (Fig. 3).

The functional connectivity during the perceptual dominance of congruent and incongruent stimuli was then compared between valence categories 400 ms before the response was made. Separate t tests were performed between positive congruent vs negative congruent; positive incongruent vs negative incongruent; positive congruent vs neutral congruent; positive incongruent vs neutral incongruent; negative congruent vs neutral congruent and finally negative incongruent vs neutral incongruent. A significant difference in functional connectivity was found only when the comparisons were made between positive and negative incongruent percepts. The connectivity between the parahippocampal gyrus and middle frontal gyrus in LA 2 (supplementary data Table 3) band was significantly lower for negative incongruent than positive incongruent percepts (at p = 0.05, t = 4.223).

**Discussion**

The study was designed to explore the differences in functional connectivity during the perceptual processing of schema congruent and incongruent visual scenes within and between specific valence categories. To the best of our knowledge, no study measured the differential functional connectivity during the perceptual dominance of emotional congruent and incongruent object-context associations.

In the current investigation, when the comparisons were made between congruent and incongruent percepts within each valence category, a significant difference in connectivity was observed only within negative valence, a heavily loaded stimulus from a survival point of view. As mentioned in our earlier study (Zacharia et al., 2020a), this could be due to a valence-congruence interaction in such a way that a combination of negative valence and incongruency in the negative incongruent stimuli is making the networks involved strikingly different from that of negative congruent stimuli. To pinpoint what happens when the valence is positive or neutral requires more studies with a similar methodology or maybe a different time window.

Within the negative category, all the area pairs which showed significant differences were having lower functional connectivity during the perceptual dominance of incongruent compared to congruent stimuli. When two neuronal populations are highly coherent, the rhythmic opening of their communication windows is expected to be synchronous. Specifically, for communication between neuronal assemblies, a message is effective for a receiving neuronal group only when the sending neuronal group’s output is so timed that it arrives at the receiving group when it is excitable. Therefore, the stronger the coherence, the more flexible the communication structure (Bowyer, 2016). Further, the associations in the congruent stimuli are already represented in the brain as schema because of our experience with them whereas incongruent associations lack a schema. Thus, the observed lower functional connectivity for incongruent percepts indicates that effective neural communication was better for congruent than incongruent association, probably because of the presence of an already established schema for congruent stimuli. The absence of such a representation for incongruent association might be hampering effective dynamic communication which might cause the consistently reported impaired cognitive performance when faced with incongruity.

In the negative valence category, a maximum number of area pairs showed the difference in the LA 1 band (68 pairs), then in beta (39 pairs) followed by UA (34 pairs), theta (15 pairs), and LA2 (5 pairs) band. This indicates that the difference in functional connectivity between congruent and incongruent percepts is more evident when the electrical communication proceeds in the LA1, beta, and UA frequency range, and

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**Fig. 3.** Paired connectivity. Figure showing the number of area pairs which showed a significantly decreased functional connectivity for incongruent percepts than congruent percepts within the negative valence category in A) 15 pairs of areas in theta; B) 68 pairs of areas in LA1; C) 5 pairs of areas in LA2; D) 34 pairs of areas in UA and E) 39 pairs of areas in beta bands. The sources are plotted as inferior view of the cortex. The scale present at the bottom of the figure shows the range in which the t-values in the comparison varied. Red lines represent lower coherence and blue lines represent higher coherence for the incongruent condition when compared to congruent conditions.
In the LA 1 band, out of 68 area pairs that showed a difference in connectivity (supplementary data Table 2), we have taken out those areas which were making functional connections with more than one area, and those areas are called nodal areas (voxel matched). In the LA 1 band, the main nodal areas were the postcentral gyrus, paracentral lobule, precuneus, middle frontal gyrus, precentral gyrus, inferior frontal gyrus, cuneus, lingual gyrus, middle temporal gyrus, transverse temporal gyrus (supplementary data Table 4).

The connectivity between the postcentral gyrus, an area associated with sensory processing (Bigbee, 2011) with the movement-related precentral gyrus (Jennenerod, 1994); emotion and conflict processing anterior cingulate gyrus (Bush et al., 2000) and memory processing inferior parietal lobule (O'Connor et al., 2010) was found to be significantly lower during the perceptual dominance of incongruent than congruent perceptions. The next nodal area, the paracentral lobule, which plays an important role in both sensory processing and motor response (Jennenerod, 1994; Pfurtscherl and Neuper, 1997), was found to be significantly less coherent with precentral gyrus which participates in recognition memory and processing of imaginable stimuli (Cavanna and Trimble, 2006; Fletcher et al., 1996); emotion, memory, novelty, and usefulness processing areas such as posterior cingulate gyrus (Rolls, 2019) and middle temporal gyrus (Ren et al., 2020); with fusiform gyrus (Kawasaki et al., 2012) and parahippocampal gyrus which are involved in object-context processing (Aminoff et al., 2007; Bar et al., 2008) during the perceptual dominance of incongruent stimuli. Further, precuneus was observed to have lower functional connections with the superior frontal gyrus which deals with attention and incongruence detection (Ganis and Kutas, 2003; Mudrik et al., 2010; Nagahama et al., 1999), parahippocampal gyrus, fusiform gyrus, and middle temporal gyrus during incongruent perception. Similarly, the middle frontal gyrus, an area involved in attention, memory, and detection of incongruence (Fairvre et al., 2019; Japee et al., 2015; Rémy et al., 2014; Yamasaki et al., 2002) showed lower functional connectivity with the postcentral gyrus, middle temporal gyrus, and inferior frontal gyrus which are involved in watching movement-related scenes, incongruence detection, emotion processing, attention, and memory (Aming et al., 2010; Milham et al., 2001; Rémy et al., 2014) during incongruent perception. The next nodal area which was found to have a significant difference in functional connectivity with more than one area was the precentral gyrus. The connectivity between the precentral gyrus and areas associated with attention, memory, and incongruence detection such as the parahippocampal gyrus and superior and inferior frontal gyri was significantly less during the perceptual dominance of incongruent stimuli. Further, the inferior frontal gyrus was found to have lower functional connectivity with areas processing attention, memory, incongruence, and emotion such as the superior frontal gyrus, parahippocampal gyrus, and posterior cingulate gyrus. Similarly, the cuneus, an important area required for visual processing (Vanni et al., 2001) also exhibited lower functional connectivity with the superior temporal gyrus which is involved in visual processing and visual search (Ellison, 2004; Karnath, 2001); parahippocampal gyrus; and inferior frontal gyrus during incongruent than congruent perception. The next nodal area was the lingual gyrus, which plays an important role in the processing of emotion, especially negative valence (Taylor et al., 1998; Wang et al., 2017). The functional connectivity between the lingual gyrus and parahippocampal gyrus; fusiform gyrus; and inferior frontal gyrus was found to be significantly less during incongruent perception. The middle temporal gyrus also showed lower functional connectivity with the parahippocampal gyrus and inferior frontal gyrus. Further, the emotion-processing area, transverse temporal gyrus (Bekinscheit, 2004; Craig, 2009; Menon and Uddin, 2010) also showed decreased functional connections with areas involved in emotion-processing and recognition memory networks such as the superior temporal gyrus, posterior cingulate gyrus, and precuneus during the perceptual dominance of incongruent than congruent stimuli.

In the UA band, 34 area pairs (supplementary data Table 2) showed significantly lower coherence for incongruent percepts when compared to congruent percepts. The main nodal areas were the postcentral gyrus, precentral gyrus, paracentral lobule, posterior cingulate gyrus, inferior parietal lobule, and middle frontal gyrus (supplementary data Table 4). The postcentral gyrus, which is essential for sensory processing, showed significantly lower functional connectivity with superior and middle frontal regions which are involved in attention, memory, and incongruence processing during the perceptual dominance of incongruent percepts than congruent percepts. Further, the connectivity between the postcentral gyrus and precuneus which is a part of the recognition memory network and the processing of the imaginable stimuli, as well as between the postcentral gyrus and posterior cingulate gyrus which is essential for emotion processing was also found to be significantly lower for incongruent than congruent percepts. Similarly, the precentral gyrus, an area that fires even while watching images that contain movement, was found to be significantly less coherent with the superior temporal gyrus which is required for emotion processing as well as with the postcentral gyrus which is essential for sensory processing during incongruent perception. The next area which was found to have a significant difference in coherence with more than one area was the paracentral lobule. The paracentral lobule is involved in both sensory and motor processing. The functional connections between the paracentral lobule with areas that participate in recognition memory networks, movement, emotion, attention, and semantic processing such as precuneus, precentral, postcentral, insula, lingual, superior frontal, and inferior parietal lobule was significantly low for incongruent percepts than congruent percepts. The emotion processing area, namely, the posterior cingulate gyrus also showed lower functional connections during incongruent perception with areas that handle memory and semantic processing such as the inferior parietal lobule and also with precuneus. Further, the inferior parietal lobule was found to be less coherent with the postcentral, precuneus, and middle frontal gyrus. These are the areas involved in emotion, attention, recognition memory, and incongruence detection. Here, the functional connectivity was low during the perceptual dominance of incongruent rather than congruent perceptions. Further, the middle frontal gyrus showed lower connectivity with the parahippocampal and precentral gyrus. The middle frontal gyrus is involved in the processing of attention, emotion, and incongruence. The parahippocampal gyrus plays an important role in object context processing and the precentral gyrus can be triggered by observing scenes that contain movements. In the beta frequency range, 39 pairs (supplementary data Table 2) showed a difference in functional connectivity between the congruent and incongruent stimuli. Here, the main nodal areas were precentral, middle frontal, cingulate, medial frontal, and parahippocampal gyri (supplementary data Table 4). The connectivity between the precentral gyrus and precuneus; inferior frontal gyrus; middle frontal gyrus; and middle temporal gyrus was found to be significantly low for incongruent percepts when compared with congruent percepts. As discussed earlier, precentral areas can be triggered by watching images containing movements. Precuneus is associated with the recognition of familiar stimuli. Inferior and middle frontal gyri are required for attention, memory, and detection of incongruence. The middle temporal gyrus is also involved in the processing of emotion. Further, the middle frontal gyrus was found to have lower connectivity with the parahippocampal area, an area required for object-context processing, and with the inferior frontal gyrus which is necessary for attentional processing during incongruent perception when compared to the congruent perception. Similarly, the cingulate gyri, an important area required for the processing of emotion, also showed lower connectivity with the superior frontal gyrus and parahippocampal gyrus during incongruent perception than congruent perception. Further, the medial frontal region showed significantly lower connectivity with the anterior cingulate gyrus, the error processing device of the brain, and with the superior frontal gyrus and transverse temporal gyrus, areas important for attention and emotion processing. The next nodal area was the parahippocampal gyrus. The functional connectivity between the parahippocampal gyrus and anterior cingulate gyrus and that
between the parahippocampal gyrus and inferior parietal lobule was also significantly low during the perceptual dominance of incongruent than congruent stimuli.

Comparisons were also performed between different valence categories. The rivalry was always happening between congruent and incongruent picture pairs of the same valence. At no point in time stimuli belonging to different valence categories were used in combination as the rivaling pair. Between valence comparisons were done in such a way that dominant congruent or incongruent stimuli during their perceptual dominance were separated based on their associated valence and compared separately for congruent percepts and incongruent percepts. A significant difference in connectivity was found only between negative incongruent and positive incongruent percepts in the LA2 band. Here again, the functional connectivity between the parahippocampal gyrus and the middle frontal gyrus was significantly lower for negative incongruent percepts. The parahippocampal gyrus is essential for the processing of object-context associations and the middle frontal gyrus for attentional processes as well for incongruence detection.

Together, these results suggest a valence-specific difference in the functional connectivity between schema-congruent and incongruent object context associations. The difference in functional connections was significant only when the associated valence was negative and within the negative category, areas related to the processing of emotion, attention, memory, semantic relations, visual processing, observation of movement, and recognition memory showed strikingly low functional connectivity between each other during the perceptual dominance of incongruent stimuli compared to the corresponding congruent stimuli. Though the difference was significant in theta and LA2 bands, a maximum number of area pairs showed the difference in LA1, UA, and beta frequency bands. Comparisons between valence categories showed significant difference only when the comparison was made between positive and negative incongruent percepts. Here again, the difference in connectivity was evident only between positive and negative incongruent percepts, and the functional connections between areas involved in the processing object-context association, attention, and incongruence were significantly low during negative incongruent perception than positive incongruent perception.

Conclusion

The current investigation was conducted to explore the valence-specific differences in the functional connections during the perceptual dominance of congruent and incongruent object-context associations while the subject performed an intermittent BR task. A significant difference in functional connectivity was observed between congruent and incongruent associations only when associated with negative valence. The functional connections were significantly lower for negative incongruent than negative congruent percepts. The areas which showed lower functional connectivity were associated with the processing of emotion, attention, memory, semantic relations, visual processing, observation of movement, and recognition memory which is required for the processing of emotional congruent and incongruent stimuli used for the investigation. The difference in functional connectivity was maximum in LA1, UA, and beta frequency ranges. Further, negative incongruent percepts were found to have significantly lower functional connectivity between the areas processing attention, incongruence, and object-context association compared to positive incongruent percepts in the LA2 band. Therefore, we propose that the functional connectivity is distinctly low during the perceptual processing of incongruent object-context associations when connected with negative valence and this could be the possible reason behind the consistently reported performance reduction when faced with incongruity in visual object identification/categorying tasks, especially which involve negatively charged stimuli.

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CRediT authorship contribution statement

Angel Anna Zacharia: Conceptualization, Designing, Methodology, Data analysis, Interpreting the results, Writing – original draft. Simran Kaur: Designing and Methodology, Writing – review & editing the manuscript; Ratna Sharma: Conceptualization, Designing and Methodology, Interpreting the results, Writing – review & editing the manuscript, Supervision.

Conflict of interest

The authors declare no conflict of interest.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi.org/10.1016/j.ibineur.2022.11.006.

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