
We hardly notice our eye blinks, yet an externally generated retinal interruption of a similar duration is perceptually salient. We examined the neural correlates of this perceptual distinction using intracranially measured ECoG signals from human visual cortex in 14 patients. In early visual areas (V1 and V2), the disappearance of the stimulus due to either invisible blinks or salient blank video frames ('gaps') led to a similar drop in activity level, followed by a positive overshoot beyond baseline, triggered by stimulus reappearance. Ascending the visual hierarchy, the reappearance-related overshoot gradually subsided for blinks but not for gaps. By contrast, the disappearance-related drop did not follow the perceptual distinction - it was actually slightly more pronounced for blinks than for gaps. These findings suggest that blinks' limited visibility compared with gaps is correlated with suppression of blink-related visual activity transients, rather than with 'filling-in' of the occluded content during blinks.


When attention is directed to stimuli in a given modality and location, information processing in other irrelevant modalities at this location is affected too. This spread of attention to irrelevant stimuli is often interpreted as superiority of location selection over modality selection. However, this conclusion is based on experimental paradigms in which spatial attention was transient whereas intermodal attention was sustained. Furthermore, whether modality selection affects processing in the task-relevant modality at irrelevant locations remains an open question. Here, we addressed effects of simultaneous spatial and intermodal attention in an EEG study using a balanced design where spatial attention was transient and intermodal attention sustained or vice versa. Effects of spatial attention were not affected by which modality was attended and effects of intermodal attention were not affected by whether the stimuli were at the attended location or not. This suggests not only spread of spatial attention to task-irrelevant modalities but also spread of intermodal attention to task-irrelevant locations. Whether spatial attention was transient or sustained did not alter the effect of spatial attention on visual N1 and Nd1 responses. Prestimulus preparatory occipital alpha band responses were affected by both transient and sustained spatial cueing, whereas late poststimulus responses were more strongly affected by sustained than by transient spatial attention. Sustained but not transient intermodal attention affected late responses (>200 msec) to visual stimuli. Together, the results undermine the universal superiority of spatial attention and suggest that the mode of attention manipulation is an important factor determining attention effects.

Deouell, LY. 2016. Microsaccades mediate a bottom-up mechanism for cross-frequency coupling in early visual cortex (Commentary on Lowet et al.). The European journal of neuroscience.
Predictive coding theories posit that neural networks learn statistical regularities in the environment for comparison with actual outcomes, signaling a prediction error (PE) when sensory deviation occurs. PE studies in audition have capitalized on low-frequency event-related potentials (LF-ERPs), such as the mismatch negativity. However, local cortical activity is well-indexed by higher-frequency bands [high-γ band (Hγ): 80-150 Hz]. We compared patterns of human Hγ and LF-ERPs in deviance detection using electrocorticographic recordings from subdural electrodes over frontal and temporal cortices. Patients listened to trains of task-irrelevant tones in two conditions differing in the predictability of a deviation from repetitive background stimuli (fully predictable vs. unpredictable deviants). We found deviance-related responses in both frequency bands over lateral temporal and inferior frontal cortex, with an earlier latency for Hγ than for LF-ERPs. Critically, frontal Hγ activity but not LF-ERPs discriminated between fully predictable and unpredictable changes, with frontal cortex sensitive to unpredictable events. The results highlight the role of frontal cortex and Hγ activity in deviance detection and PE generation.

Environmental rhythms potently drive predictive resource allocation in time, typically leading to perceptual and motor benefits for on-beat, relative to off-beat, times, even if the rhythmic stream is not intentionally used. In two human EEG experiments, we investigated the behavioral and electrophysiological expressions of using rhythms to direct resources away from on-beat times. This allowed us to distinguish goal-directed attention from the automatic capture of attention by rhythms. The following three conditions were compared: (1) a rhythmic stream with targets appearing frequently at a fixed off-beat position; (2) a rhythmic stream with targets appearing frequently at on-beat times; and (3) a nonrhythmic stream with matched target intervals. Shifting resources away from on-beat times was expressed in the slowing of responses to on-beat targets, but not in the facilitation of off-beat targets. The shifting of resources was accompanied by anticipatory adjustment of the contingent negative variation (CNV) buildup toward the expected off-beat time. In the second experiment, off-beat times were jittered, resulting in a similar CNV adjustment and also in preparatory amplitude reduction of beta-band activity. Thus, the CNV and beta activity track the relevance of time points and not the rhythm, given sufficient incentive. Furthermore, the effects of task relevance (appearing in a task-relevant vs irrelevant time) and rhythm (appearing on beat vs off beat) had additive behavioral effects and also dissociable neural manifestations in target-evoked activity: rhythm affected the target response as early as the P1 component, while relevance affected only the later N2 and P3. Thus, these two factors operate by distinct mechanisms.

Abstract

In situations of choice between uncertain options, one might get feedback on both the outcome of the chosen option and the outcome of the unchosen option ("the alternative"). Extensive research has shown that when both outcomes are eventually revealed, the alternative's outcome influences the way people evaluate their own outcome. In a series of experiments, we examined whether the outcome of the alternative plays an additional role in the decision-making process by creating expectations regarding the outcome of the chosen option. Specifically, we hypothesized that people see a good (bad) alternative’s outcome as a bad (good) sign regarding their own outcome when the two outcomes are in fact uncorrelated, a phenomenon we call the "Alternative Omen Effect" (ALOE). Subjects had to repeatedly choose between two boxes, the outcomes of which were then sequentially revealed. In Experiments 1 and 2 the alternative's outcome was presented first, and we assessed the individual's prediction of their own outcome. In Experiment 3, subjects had to predict the alternative's outcome after seeing their own. We find that even though the two outcomes were in fact uncorrelated, people tended to see a good (bad) alternative outcome as a bad (good) sign regarding their own outcome. Importantly, this illusory negative correlation affected subsequent behavior and led to irrational choices. Furthermore, the order of presentation was critical: when the outcome of the chosen option was presented first, the effect disappeared, suggesting that this illusory negative correlation is influenced by self-relevance. We discuss the possible sources of this illusory correlation as well as its implications for research on counterfactual thinking.


Adapting classifiers for the purpose of brain signal decoding is a major challenge in brain-computer-interface (BCI) research. In a previous study we showed in principle that hidden Markov models (HMM) are a suitable alternative to the well-studied static classifiers. However, since we investigated a rather straightforward task, advantages from modeling of the signal could not be assessed.


Intending to perform an action and then immediately executing it is a mundane process. The cognitive and neural mechanisms involved in this process of "proximal" intention formation and execution, in the face of multiple options to choose from, are not clear, however. Especially, it is not clear how intentions are formed when the choice makes no difference. Here we used behavioral and electrophysiological measures to investigate the temporal dynamics of proximal intention formation and "change of intention" in a free picking scenario, in which the alternatives are on a par for the participant. Participants pressed a right or left button following either an instructive visible arrow cue or a visible neutral "free-choice" cue, both preceded by a masked arrow prime. The goal of the prime was to induce a bias toward pressing the left or right button. Presumably, when the choice is arbitrary, such bias should determine the decision. EEG
lateralized readiness potentials and EMG measurements revealed that the prime indeed induced an intention to move in one direction. However, we discovered a signature of "change of intention" in both the Instructed and Free-choice decisions. These results suggest that, even in arbitrary choices, biases present in the neural system for choosing one or another option may be overruled and point to a curious "picking deliberation" phenomenon. We discuss a possible neural scenario that could explain this phenomenon.

2014


Whether contextual regularities facilitate perceptual stages of scene processing is widely debated, and empirical evidence is still inconclusive. Specifically, it was recently suggested that contextual violations affect early processing of a scene only when the incongruent object and the scene are presented asynchronously, creating expectations. We compared event-related potentials (ERPs) evoked by scenes that depicted a person performing an action using either a congruent or an incongruent object (e.g., a man shaving with a razor or with a fork) when scene and object were presented simultaneously. We also explored the role of attention in contextual processing by using a pre-cue to direct subjects’ attention towards or away from the congruent/incongruent object. Subjects’ task was to determine how many hands the person in the picture used in order to perform the action. We replicated our previous findings of frontocentral negativity for incongruent scenes that started ~210ms post stimulus presentation, even earlier than previously found. Surprisingly, this incongruency ERP effect was negatively correlated with the reaction times cost on incongruent scenes. The results did not allow us to draw conclusions about the role of attention in detecting the regularity, due to a weak attention manipulation. By replicating the 200-300ms incongruity effect with a new group of subjects at even earlier latencies than previously reported, the results strengthen the evidence for contextual processing during this time window even when simultaneous presentation of the scene and object prevent the formation of prior expectations. We discuss possible methodological limitations that may account for previous failures to find this an effect, and conclude that contextual information affects object model selection processes prior to full object identification, with semantic knowledge activation stages unfolding only later on.


Exposure to rhythmic stimulation results in facilitated responses to events that appear in-phase with the rhythm and modulation of anticipatory and target-evoked brain activity, presumably reflecting "exogenous," unintentional temporal expectations. However, the extent to which this effect is independent from intentional processes is not clear. In two EEG experiments, we isolated the unintentional component of this effect from high-level, intentional factors. Visual targets were presented either in-phase or out-of-phase with regularly flickering colored stimuli. In different blocks, the rhythm could be predictive (i.e., high probability for in-phase target) or not, and the color could be predictive (i.e., valid cue the interval to the target) or not. Exposure to nonpredictive rhythms resulted in faster responses for in-phase targets, even when the color predicted specific out-of-phase target times. Also, the contingent negative variation, an EEG component reflecting temporal anticipation, followed the interval of the nonpredictive rhythm and not that of the predictive color. Thus, rhythmic stimulation unintentionally induced expectations, even when this was detrimental. Intentional usage of predictive rhythms to form expectations resulted in a stronger
behavioral effect, and only predictive cues modulated the latency of the target-evoked P3, presumably reflecting stimulus evaluation. These findings establish the existence of unintentional temporal expectations in rhythmic contexts, dissociate them from intentional expectations, and highlight the need to distinguish between the source of expectation (exogenous-endogenous) and the level of voluntary control involved in it (unintentional-intentional).


Brain computer interface applications, developed for both healthy and clinical populations, critically depend on decoding brain activity in single trials. The goal of the present study was to detect distinctive spatiotemporal brain patterns within a set of event related responses. We introduce a novel classification algorithm, the spatially weighted FLD-PCA (SWFP), which is based on a two-step linear classification of event-related responses, using fisher linear discriminant (FLD) classifier and principal component analysis (PCA) for dimensionality reduction. As a benchmark algorithm, we consider the hierarchical discriminant component Analysis (HDCA), introduced by Parra, et al. 2007. We also consider a modified version of the HDCA, namely the hierarchical discriminant principal component analysis algorithm (HDPCA). We compare single-trial classification accuracies of all the three algorithms, each applied to detect target images within a rapid serial visual presentation (RSVP, 10 Hz) of images from five different object categories, based on single-trial brain responses. We find a systematic superiority of our classification algorithm in the tested paradigm. Additionally, HDPCA significantly increases classification accuracies compared to the HDCA. Finally, we show that presenting several repetitions of the same image exemplars improve accuracy, and thus may be important in cases where high accuracy is crucial.


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Functional magnetic resonance imaging (fMRI) findings suggest that a part of the planum temporale (PT) is involved in representing spatial properties of acoustic information. Here, we tested whether this representation of space is frequency-dependent or generalizes across spectral content, as required from high order sensory representations. Using sounds with two different spectral content and two spatial locations in individually tailored virtual acoustic environment, we compared three conditions in a sparse-fMRI experiment: Single Location, in which two sounds were both presented from one location; Fixed Mapping, in which there was one-to-one mapping between two sounds and two locations; and Mixed Mapping, in which the two sounds were equally likely to appear at either one of the two locations. We surmised that only neurons tuned to both location and frequency should be differentially adapted by the Mixed and Fixed mappings. Replicating our previous findings, we found adaptation to spatial location in the PT. Importantly, activation was higher for Mixed Mapping than for Fixed Mapping blocks, even though the two sounds and the two locations appeared equally in both conditions. These results show that spatially tuned neurons in the human PT are not invariant to the spectral content of sounds.

Bonato, M, Deouell LY. 2013 Hemispatial neglect: computer-based testing allows more sensitive quantification of attentional disorders and recovery and might lead to better evaluation of rehabilitation. Frontiers in human neuroscience. 7:162.

Shalgi, S, Deouell LY. 2013 Is there any electrophysiological evidence for subliminal error processing? Frontiers in neuroscience. 7:150.

The role of error awareness in executive control and modification of behavior is not fully understood. In line with many recent studies showing that conscious awareness is unnecessary for numerous high-level processes such as strategic adjustments and decision making, it was suggested that error detection can also take place unconsciously. The Error Negativity (Ne) component, long established as a robust error-related component that differentiates between correct responses and errors, was a fine candidate to test this notion: if an Ne is elicited also by errors which are not consciously detected, it would imply a subliminal process involved in error monitoring that does not necessarily lead to conscious awareness of the error. Indeed, for the past decade, the repeated finding of a similar Ne for errors which became aware and errors that did not achieve awareness, compared to the smaller negativity elicited by correct responses (Correct Response Negativity; CRN), has lent the Ne the prestigious status of an index of subliminal error processing. However, there were several notable exceptions to these findings. The study in the focus of this review (Shalgi and Deouell, 2012) sheds new light on both types of previous results. We found that error detection as reflected by the Ne is correlated with subjective awareness: when awareness (or more importantly lack thereof) is more strictly determined using the wagering paradigm, no Ne is elicited without awareness. This result effectively resolves the issue of why there are many conflicting findings regarding the Ne and error awareness. The average Ne amplitude appears to be influenced by individual criteria for error reporting and therefore, studies containing different mixtures of participants who are more confident of their own performance or less confident, or paradigms that either encourage or don’t encourage reporting low confidence errors will show different results. Based on this evidence, it is no longer possible
to unquestioningly uphold the notion that the amplitude of the Ne is unrelated to subjective awareness, and therefore, that errors are detected without conscious awareness.

2012


The Error-Related Negativity (Ne or ERN) is a reliable electrophysiological index of error processing, which has been found to be independent of whether a subject is aware of an error or not. A large Ne was equally seen after errors that were consciously detected (Aware errors) and those that were not (Unaware errors), compared to a small negativity for correct responses (CRN). This suggests a dissociation between an automatic, preconscious error processing mechanism and subjective evaluation. A common concern regarding this finding is that subjects could have been somewhat aware of their errors, but did not report them due to lack of confidence. Here we tested this possibility directly using a betting paradigm which allowed us to separate occasions in which the subjects were confident of their response and trials in which they were unsure. In a choice reaction time task, subjects directly judged the accuracy of each response (correct or error) and then bet on this judgment using a high, medium, or low amount of money. The bets were used to determine the level of confidence the subjects had of their response. The average across all subjects regardless of confidence (betting) measure replicated the reported finding of an equal Ne for Aware and Unaware errors which was larger than the CRN. However, when Ne measurement was confined to high confidence (high bet) trials in confident subjects, a prominent Ne was seen only for Aware errors, while confident Unaware errors (i.e., error trials on which subjects made high bets that they were correct) elicited a response that did not differ from the CRN elicited by truly correct answers. In contrast, for low confidence trials in unconfident subjects, an intermediate and equal Ne/CRN was elicited by CRN, Aware and Unaware errors. These results provide direct evidence that the Ne is related to error awareness, and suggest the amplitude of the Ne/CRN depends on individual differences in error reporting and confidence.

2011

Schechtman, E, Shrem T, Deouell LY. 2012Spatial Localization of Auditory Stimuli in Human Auditory Cortex is Based on Both Head-Independent and Head-Centered Coordinate Systems. The Journal of Neuroscience. 32:13501-13509. Abstract

In humans, whose ears are fixed on the head, auditory stimuli are initially registered in space relative to the head. Eventually, locations of sound sources need to be encoded also relative to the body, or in absolute allocentric space, to allow orientation toward the sounds sources and consequent action. We can therefore distinguish between two spatial representation systems: a basic head-centered coordinate system and a more complex head-independent system. In an ERP experiment, we attempted to reveal which of these two coordinate systems is represented in the human auditory cortex. We dissociated the two systems using the mismatch negativity (MMN), a well studied EEG effect evoked by acoustic deviations. Contrary to previous findings suggesting that only primary head-related information is present at this early stage of processing, we observed significant MMN effects for both head-independent and head-centered deviant stimuli. Our findings thus reveal that both primary head-related and secondary body- or world-related reference frames are represented at this stage of auditory processing.
The recent discovery of incessant spontaneous fluctuations in human brain activity (also termed resting state fMRI) has been a focus of intense research in brain imaging. The spontaneous BOLD activity shows organized anatomical specialization as well as disruption in a number of brain pathologies. The link between the spontaneous fMRI fluctuations and human behavior is therefore of acute interest and importance. Here we report that a highly significant correlation exists between spontaneous BOLD fluctuations and eye movements which occur subliminally and spontaneously in the absence of any visual stimulation. Of the various eye movement parameters tested, we found robust and anatomically consistent correlations with both the amplitude and velocity of spontaneous eye movements. Control experiments ruled out a contribution of spatial and visual attention as well as smooth pursuit eye movements to the effect. The consistent anatomical specificity of the correlation patterns and their tight temporal link at the proper hemodynamic delay argues against a non-neuronal explanation of the effect, such as cardiac or respiratory cycles. Our results thus demonstrate a link between resting state and spontaneously emerging subconscious oculo-motor behavior.

Event-related potentials offer evidence for face distinctive neural activity that peaks at about 170 ms following the onset of face stimuli (the N170 effect). We investigated the role of the perceptual mechanism reflected by the N170 effect by comparing the adaptation of the N170 amplitude when target faces were preceded either by identical face images or by different faces relative to when they were preceded by objects. In two experiments, we demonstrate that the N170 is equally adapted by repetition of the same or different faces. Thus, our findings show that the N170 is sensitive to the category rather than the identity of a face. This outcome supports the hypothesis that the N170 effect reflects the activity of a perceptual mechanism which discriminates faces from objects and streams face stimuli to dedicated circuits, specialized in encoding and decoding information about the face.

We previously showed that the transient broadband induced gamma-band response in EEG (iGBRtb) appearing around 200-300 ms following a visual stimulus reflects the contraction of extra-ocular muscles involved in the execution of saccades, rather than neural oscillations. Several previous studies reported induced gamma-band responses also following auditory stimulation. It is still an open question whether, similarly to visual paradigms, such auditory paradigms are also sensitive to the saccadic confound. In the current study we address this question using simultaneous eye-tracking and EEG recordings during an auditory oddball paradigm. Subjects were instructed to respond to a rare target defined by sound source location, while fixating on a central screen. Results show that, similar to what was found in visual paradigms, saccadic rate displayed typical temporal dynamics including a post-stimulus decrease followed by an increase. This increase was more moderate, had a longer latency, and was less consistent across subjects than was found in the visual case. Crucially, the temporal dynamics of the induced gamma response were similar to those of saccadic-rate modulation. This suggests that the auditory induced
gamma-band responses recorded on the scalp may also be affected by saccadic muscle activity.


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Human conscious awareness is commonly seen as the climax of evolution. However, what function-if any-it serves in human behavior is still debated. One of the leading suggestions is that the cardinal function of conscious awareness is to integrate numerous inputs-including the multitude of features and objects in a complex scene-across different levels of analysis into a unified, coherent, and meaningful perceptual experience. Here we demonstrate, however, that integration of objects with their background scenes can be achieved without awareness of either. We used a binocular rivalry technique known as continuous flash suppression to induce perceptual suppression in a group of human observers. Complex scenes that included incongruent objects escaped perceptual suppression faster than normal scenes did. We conclude that visual awareness is not needed for object-background integration or for processing the likelihood of an object to appear within a given semantic context, but may be needed for dealing with novel situations.


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It is well established that cognitive system overload is reflected in the attentional blink (AB), the failure to report a second target when it closely follows detection of a first target within a rapid series of stimuli. However, there is intense controversy concerning the effect of first-target detection in one modality on subsequent dynamics of attentional resources in other modalities. Mixed results were found using an audiovisual AB paradigm: depletion of resources in one modality either impaired performance in the other modality or had no effect. Here, we circumvent the need for task switching by measuring an event-related potential, the mismatch negativity, which reflects implicit auditory change detection without requiring task engagement and is present even for background sounds that participants ignore. Surprisingly, we find that during the visual AB, auditory processing is enhanced rather than inhibited, as would be expected by system overload. We suggest that multimodal attentional resources may be freed rather than engaged during the visual AB. Suppression of irrelevant input may require active control by a central executive, which is preoccupied during the visual AB, and/or there may be no reason to suppress other-modal input since the visual system will miss its second target anyway.


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Contextual regularities, that is, objects' tendency to appear with certain other objects, facilitate the processing of visual scenes and confer contextually incongruent objects with a special attentional status. This study was aimed at investigating the mechanisms underlying this attentional advantage using Binocular Rivalry (BR). In two experiments, congruent and incongruent images (e.g., a man drinking from a glass vs. a man "drinking" from a hairbrush) were pitted against each other, yielding a version of BR in which two objects rival within a given scene. Incongruent objects predominated in awareness longer than congruent ones. This effect stemmed from the fact that their dominance epochs lasted longer on the average than those of congruent objects, suggesting a difficulty to disengage attention from such objects. On the other hand, no support was found for the notion that incongruent objects also attract attention.
Amihai, I., Deouell, L., Bentin, S. 2010. **Conscious awareness is necessary for processing race and gender information from faces.** Consciousness and cognition. Abstract

Previous studies suggested that emotions can be correctly interpreted from facial expressions in the absence of conscious awareness of the face. Our goal was to explore whether subordinate information about a face's gender and race could also become available without awareness of the face. Participants classified the race or the gender of unfamiliar faces that were ambiguous with regard to these dimensions. The ambiguous faces were preceded by face-images that unequivocally represented gender and race, rendered consciously invisible by simultaneous continuous-flash-suppression. The classification of ambiguous faces was biased away from the category of the adaptor only when it was consciously visible. The duration of subjective visibility correlated with the aftereffect strength. Moreover, face identity was consequential only if consciously perceived. These results suggest that while conscious awareness is not needed for basic level categorization, it is needed for subordinate categorization. Emotional information might be unique in this respect.
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