NeuroImage 66 (2013) 261–269

Contents lists available at SciVerse ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg

Priming of visual cortex by temporal attention? The effects of temporal predictability on stimulus(-specific) processing in early visual cortical areas ☆

Rico Fischer *, Franziska Plessow, Hannes Ruge

Technische Universität Dresden, Germany

ARTICLE INFO

Article history:
Accepted 30 October 2012
Available online 8 November 2012

Keywords:
Temporal predictability
Temporal attention
Alerting signal
Accessory

ABSTRACT

In recent studies it has been shown that temporal predictability of expected events alters processing in perception and action. Yet, the neural mechanism(s) by which temporal predictability biases this processing is to date little understood. Therefore, in the present fMRI study we investigated how temporal predictability affects neural processing in visual cortical areas. For this, thirty-four participants either categorized the gender or the movement direction of vertically or horizontally moving faces in different blocks of trials. Temporal predictability of stimulus onset was manipulated by the presence or absence of an auditory alerting signal validly predicting stimulus onset. The behavioral data revealed a clear performance benefit for the presence of an alerting signal. Neuroimaging results showed that irrespective of the currently performed task temporal predictability significantly reduced activation in the primary visual cortex. This activation reduction correlated with the alerting signal-related performance benefit. Furthermore, we did not find a selective influence of increased temporal predictability on target-specific visual processing (faces or movement) in the respective material-specific visual brain areas. Together, these findings suggest an increased task-unspecific readiness by the alerting signal that might result in more efficient transmission of stimulus codes into response codes.

Introduction

The successful deployment of temporal attention to the onset of an expected event is a major aspect in action control and the prerequisite for efficient interaction with and in the environment. Predicting and therefore preparing for the onset of a future event reduces temporal uncertainty and allows for an optimal engagement in information processing (Niemi and Näätänen, 1981). Thus, it is not surprising that manipulations of temporal predictability of expected events have been shown to bias perception and action (for an overview see Nobre et al., 2007). Much research has been conducted over the last decade to determine neural mechanisms responsible for allocation of attention in time (Coull, 2004; Coull et al., 2000, 2001; Fan et al., 2005; Hackley et al., 2009) and to detect similarities, for example, to allocation of attention in space (Coull and Nobre, 1998). Yet, given the importance of the ability to anticipate the onset of future events, it appears surprising that to date only little is known about the neural mechanisms by which temporal predictability might bias perception and action (cf. Nobre, 2010).

The deployment of attention (in time or space) is generally thought to support the selection of task-relevant features and thus enables selective attention. Previous research in this field has predominantly been dedicated to studying the effects of *spatial* attention on stimulus processing. The conclusion that spatial attention improves perceptual analysis can be derived from the finding that contrast perception (i.e., responding to the orientation of contrast gratings) is enhanced at the attended spatial location (Carrasco et al., 2004). Early influential work demonstrated modulating effects of spatial attention on neural activity in extrastriate neurons (area V4) in non-human primates (Moran and Desimone, 1985).

More recent evidence of selective spatial attention gating visual processing in human participants was provided by an fMRI study in which target-specific enhancement of neural activity in visual cortical areas was related to the deployment of visual spatial attention (Hopfinger et al., 2000). The selective allocation of visual attention toward a location in space includes top-down attentional control in terms of attentional disengagement and voluntary orienting. In a spatial cuing paradigm, the cue triggered the allocation of attention to the indicated location. Isolating cue-related neural activity, the authors were able to identify a network for voluntary attentional control. In addition, they also showed the consequences of allocating spatial attention. In particular, cue-related attentional control biased activity in those visual cortical areas that were later dedicated to process the visual target. In other words, the deployment of spatial attention resulted in *selective sensory processing* of relevant visual targets (Hopfinger et al., 2000).

To date, it is completely unclear to which extend such findings related to spatial attention can be generalized to the field of temporal attention, e.g., whether temporal predictability can also trigger selective

☆ This research was supported by a grant of the German Research Foundation (DFG, FI 1624/2-1).

* Corresponding author at: Department of Psychology, Technische Universität Dresden, D-01062 Dresden, Germany.
E-mail address: fischer@psychologie.tu-dresden.de (R. Fischer).

1053-8119/$ – see front matter © 2012 Elsevier Inc. All rights reserved.
http://dx.doi.org/10.1016/j.neuroimage.2012.10.091

sensory processing. It is agreed upon that temporal predictability facilitates information processing and thus optimizes behavior by speeding up performance. While traditional views propose a late locus of effects of temporal predictability at motor stages (Coull and Nobre, 1998; Kiesel and Miller, 2007; Mattes et al., 1997; Miniussi et al., 1999; Tandonnet et al., 2006), recently research has been accumulated demonstrating effects of temporal predictability on early perceptual and pre-motor stages of information processing (Correa et al., 2005, 2006; Hackley et al., 2007; Lange et al., 2003; Martens and Johnson, 2005; Rolke and Hofmann, 2007).

On the assumption that temporal predictability modulates perceptual processing, few studies have conducted research investigating the neural mechanisms of perceptual biases by temporal predictability. Anderson and Sheinberg (2008), for example, could show that spiking responses of neurons in the inferior temporal (IT) cortex of monkeys were modulated by manipulations of temporal predictability. In a temporal orienting task, each picture of a number of objects served as cue (indicating an early or late target onset with 80% validity) or as target (indicating the required response). For early target onset trials, a valid cue was associated with more spiking than an invalid cue. That is, the early spiking response decreased when the stimulus onset was not expected (invalid cue).

In human participants, changes in the temporal predictability of stimulus onset were found to result in altered neural processing in the primary visual cortex (V1, Alink et al., 2010; see also Bueti et al., 2010). Alink and colleagues, for example, argued that stimuli with a predictable onset require less neural activation to transmit its information from lower to higher cortices (Rao and Ballard, 1999). Accordingly, in an fMRI study Alink et al. (2010) showed that neural responses in V1 were smaller when the stimulus onset was temporally predictable than when it was unpredictable by participants. Although this demonstration of predictable stimuli being processed with less neural activation in visual cortical areas is an intriguing result, the predictability of stimulus onset was provided by means of the trajectory of surrounding illusory motion. It therefore remains an open question as to whether these findings can be generalized to and replicated with more conventional methods of reducing temporal uncertainty in the environment, such as explicit temporal cues predicting the stimulus onset. This is especially important since other fMRI studies demonstrated *increased* activations of the visual cortex areas such as the right occipital pole (BA 18) that were associated with exogenous shifts of temporal attention (Coull et al., 2000).

Although the research outlined above has provided important opening work on understanding the neural underpinnings of the allocation of attention to predict upcoming stimulus events, a number of important questions remain. For example, as aforementioned, can the effects of temporal predictability on early visual cortical areas as reported by Alink et al. (2010) be generalized to different kinds of temporal predicability? How selective is the sensory priming of neural activity in visual areas? Especially the latter question appears captivating. It has been argued, for example, that the selection of task-relevant information is guided by the expected temporal onset of events (Correa, 2010). Does the allocation of temporal attention to the onset of the stimulus event result in *selective sensory processing* of relevant visual targets analogously to the allocation of spatial attention (Hopfinger et al., 2000)? Indeed, spatial and temporal attention share many (neural) commonalities (Coull and Nobre, 1998) and it has been argued that orienting attention in time results in virtually the same changes in neural activity as observed for orienting attention in space suggesting that both types of allocating attention are neurophysiologically similar (cf. Anderson and Sheinberg, 2010). Therefore, while previous studies suggest a "ubiquitous system for allocating attentional resources in general" (Coull and Nobre, 1998, p.7431), it is yet to be tested whether the deployment of temporal attention to stimulus onset (temporal predictability) leads to the same consequences as the deployment of spatial attention — namely, the selective (biased) sensory processing of relevant visual targets.

The present study

The present study aims at providing further information whether and how temporal predictability of the upcoming stimulus onset affects neural processing in visual cortical areas. First, we aim at extending the findings by Alink et al. (2010) by investigating the generality of the observed reduction in neural activity of V1 neurons in response to temporal predictability. Alink and colleagues explained their finding by means of feedback signals from higher motion-related areas as temporal onset predictability in their paradigm was closely linked with motion perception. Previous studies mostly applied temporal visual cues to manipulate temporal predictability (e.g., Coull, 2004; Coull and Nobre, 1998; Fan et al., 2005), which however, may confound neural activity of target stimulus processing in V1. Therefore, we will test whether patterns of reduced neuronal activity in V1 can similarly be found when task-irrelevant *acoustic* alerting signals contain temporal information about stimulus onset.

Our second aim relates to assumptions in the domain of spatial attention proposed by Hopfinger et al. (2000). Here we follow the idea that, if not only the allocation of spatial attention but also the deployment of temporal attention results in selective sensory processing of relevant visual targets, it should be possible to obtain modulations of neural activity in stimulus-material specific neural areas in accordance with manipulations of temporal attention.

In the present study, participants were presented with pictures of male and female faces that could move either in a left-right dimension (horizontally) or in an up-down dimension (vertically). In one block of trials participants had to respond to movement direction (horizontal versus vertical) whereas in the other block of trials they had to discriminate gender (female versus male). We particularly implemented a choice-reaction task instead of often used stimulus-detection tasks, because it was suggested that effects of temporal predictability on sensory processing are more likely to be detected when a perceptual analysis of the visual stimulus features is required (cf. Correa, 2010). Temporal uncertainty was realized by large variations in the response–stimulus interval (RSI) between consecutive trials. In this context of unpredictable stimulus onset, an acoustic signal validly predicted the temporal stimulus onset in half of the trials by appearing always at a constant 250 ms prior to stimulus onset — a forperiod interval known for optimum preparation for stimulus onset (Fischer et al., 2007; Gottsdanker, 1980) and for revealing performance benefits in terms of speeded responses in a variety of choice-reaction tasks (Fischer et al., 2010, 2012). We particularly chose this manipulation of temporal predictability because 1) the presence versus absence of an alerting signal is known to determine temporal predictability (Bernstein et al., 1973) and 2) this approach allowed differentiating between neural activity of the auditory temporal cue (alerting signal) and the neural activity of visual target stimulus processing in V1. This distinguishes the current approach from more classical manipulations of temporal predictability (e.g., Coull, 2004; Coull and Nobre, 1998; Fan et al., 2005), in which the neural activity of visual temporal cue may be difficult to dissociate from neural activity of the target stimulus.

Therefore, within the present paradigm we expect alerting signal-based response speeding in the behavioral data for both, face- and motion-categorization task, alike. We also expect the alerting signal to activate the temporal orienting or alerting network that comprises a number of specified cortical areas associated with the allocation and directing of temporal attention to an expected point in time (Coull et al., 2000, 2001; Fan et al., 2005; Hackley et al., 2009; Thiel et al., 2004). Typical areas include the left intra-parietal cortex and pre-supplementary motor area (pre-SMA) possibly supporting attentional allocation towards an expected event and superior temporal