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Electrophysiological measurement of the effect of inter-stimulus competition on early cortical stages of human vision

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ABSTRACT

Competition between inputs in early visual cortex has been established as a key determinant in perception through decades of animal single cell and human fMRI research. We developed a novel ERP paradigm allowing this competition to be studied in humans, affording an opportunity to gain further insight into how competition is reflected at the neural level. Checkerboard stimuli were presented to elicit C1 (indexing processing in V1), C2 (hypothesized to reflect V1 after extrastriate feedback), and P1 (extrastriate) components. Stimuli were presented in three randomized conditions: single stimulus, near proximity pairs and far proximity pairs. Importantly, near stimuli (0.16° visual angle apart) were positioned to compete in primary visual cortex, whereas far stimuli (2° apart) were positioned to compete in extrastriate visual areas.

As predicted, the degree and spatial range of competition increased from the C1 component to the C2 and P1 components. Specifically, competitive interactions in C1 amplitude were modest and present only for near-proximity pairs, whereas substantial competition was present for the P1, even for far-proximity pairs. To our knowledge, this is the first study to measure how competition unfolds over time in human visual cortex. Importantly, this method provides an empirical means of measuring competitive interactions at specific stages of visual processing, rendering it possible to rigorously test predictions about the effects of competition on perception, attention, and working memory.

Introduction

Objects in the external world are constantly competing for representation in the human brain at different scales and in many different parts of the cortex. The resolution of this competition is a vital mechanism that serves to prevent information overload by prioritizing currently relevant information, as described in the highly influential theory of biased competition (Desimone and Duncan, 1995). As an example, competition between visual stimuli through lateral inhibition in the retina (e.g. Hartline et al., 1956; Alpern and David, 1959) has been shown to aid contrast and contour perception by sharpening visual input, and is also implicated in the organization of center-surround receptive fields in bipolar and ganglion cells (Werblin, 1974; Cook and McReynolds, 1998). Moreover, in visual cortex, recent studies suggest that competitive interactions are stronger between stimuli presented within the same visual receptive field (RF) than between stimuli presented in different RFs (Kastner et al., 1998; Reynolds et al., 1999).

Reynolds et al. (1999) demonstrated the presence of competitive interactions between stimuli within RFs using single cell recordings in primates. When an unattended stimulus pair was presented simultaneously within a single V4 RF, the firing rate was not simply the sum of the firing rates for each stimulus presented alone but was instead near the average of the firing rates for the individual stimuli. Further, when one stimulus of a pair was attended, the features of this stimulus entirely determined the cell's firing rate. Similarly, Luck et al. (1997) found that attention modulated V2 and V4 firing rates only when both the attended and ignored stimuli were inside the neuron's RF (and thus were in competition for control over that neuron). Moreover, when both stimuli were inside the RF, the attention effect was reduced when the stimuli were presented sequentially rather than simultaneously, presumably because sequential presentation reduces competition between the stimuli (see below). Other studies have also found large single-unit attention effects when both attended and ignored stimuli were simultaneously presented inside the neuron's RF (Treue and Maunsell, 1996; Moran and Desimone, 1985). It is important to note that single cell methods have been unable to investigate competitive interactions between two stimuli within the same V1 RF, due to small RF size.

In an fMRI study in humans, Kastner et al. (1998) presented the same four stimuli either simultaneously or sequentially in the periphery, while participants performed a task at fixation. They found decreased BOLD activity in response to simultaneous relative to

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sequential stimuli in areas V1, V2, V4 and TEO, with the difference between the two conditions increasing with RF size. This outcome is consistent with strong competition between stimuli that were presented simultaneously within the same RF, with more items falling within a single RF in areas with large RFs than in areas such as V1 that have small RFs (see also Kastner et al., 2001).

Studies of lateral masking and crowding (e.g., Loomis, 1978) also suggest that stimulus proximity reduces discriminability. In an early study, Flom et al. (1963) found that flanking black bars reduced participants' ability to make a judgment about peripherally presented Landolt Cs, with the interaction reduced as the distance between them increased. Flom et al. suggested this interaction was due to large receptive field sizes in peripheral vision. Indeed, a later study by Levi et al. (2002) suggests that crowding occurs more strongly for peripheral than foveal stimuli. However, it is difficult to determine from these studies whether the observed decrements in performance reflect interactions in feedforward or feedback processing.

Similarly, although Kastner et al. (1998) found evidence of inter-stimulus competition as early as V1, the poor temporal resolution of the hemodynamic response made it impossible to determine whether the V1 competition they observed reflected competition within V1 during feedforward processing or competition at later stages feeding back to V1. On the other hand, the excellent temporal resolution of the event-related potential (ERP) technique makes it ideal for assessing the different stages in visual processing at which competition can exert its effect in human neural populations and forms the basis of the present investigation.

In the present study, ERPs were used to assess the effects of inter-stimulus competition on early visual ERP components. The components of interest were: C1, thought to originate in primary visual cortex (Clark et al., 1995; Di Russo et al., 2002; Jeffreys and Axford, 1972); C2 (Fortune and Hood, 2003; Kappenman and Luck, 2012), which we suggest to reflect V1 activity after feedback from extrastriate areas; and P1, thought to reflect extrastriate areas, including area V3 and middle-occipital gyrus, and anterior V4v (Di Russo et al., 2002). Our goal was to demonstrate that ERPs can provide a temporally sensitive index of early stimulus competition at varying levels of the early visual system. This is an important first step towards being able to study how competitive interactions in early visual activity depend on bottom-up factors such as stimulus similarity and top-down factors such as attention.

Our experimental approach took advantage of the fact that voltages in the brain directly summate (Nunez and Srinivasan, 2006). Thus, if stimuli presented at two different locations are processed independently, the ERP response to the two stimuli presented simultaneously will be exactly the same as the sum of the ERP responses to the two stimuli presented individually. Consequently, if the observed ERP to two simultaneous stimuli differs from the sum of the ERPs to the individual stimuli at a given point in time, the two stimuli must be interacting with each other at that time. We therefore presented stimuli sequentially at two locations to obtain the responses to the individual stimuli and also presented the stimuli simultaneously at these two locations (see Figs. 1 and 2). This approach has been used extensively in research on binaural interactions between auditory stimuli presented simultaneously to the two ears compared with stimuli presented separately to each ear (see Pratt, 2012 for a review). We also varied the distance between the two locations so that we could test the hypothesis that interactions between stimuli would occur earlier for nearby locations than for more distant locations. Specifically, we predicted that the near stimuli would compete beginning in primary visual cortex, leading to interactions between simultaneous stimuli beginning with the C1 wave. The far stimuli were predicted to compete only in later visual areas, leading to interactions in the P1 wave but not in the C1 wave.

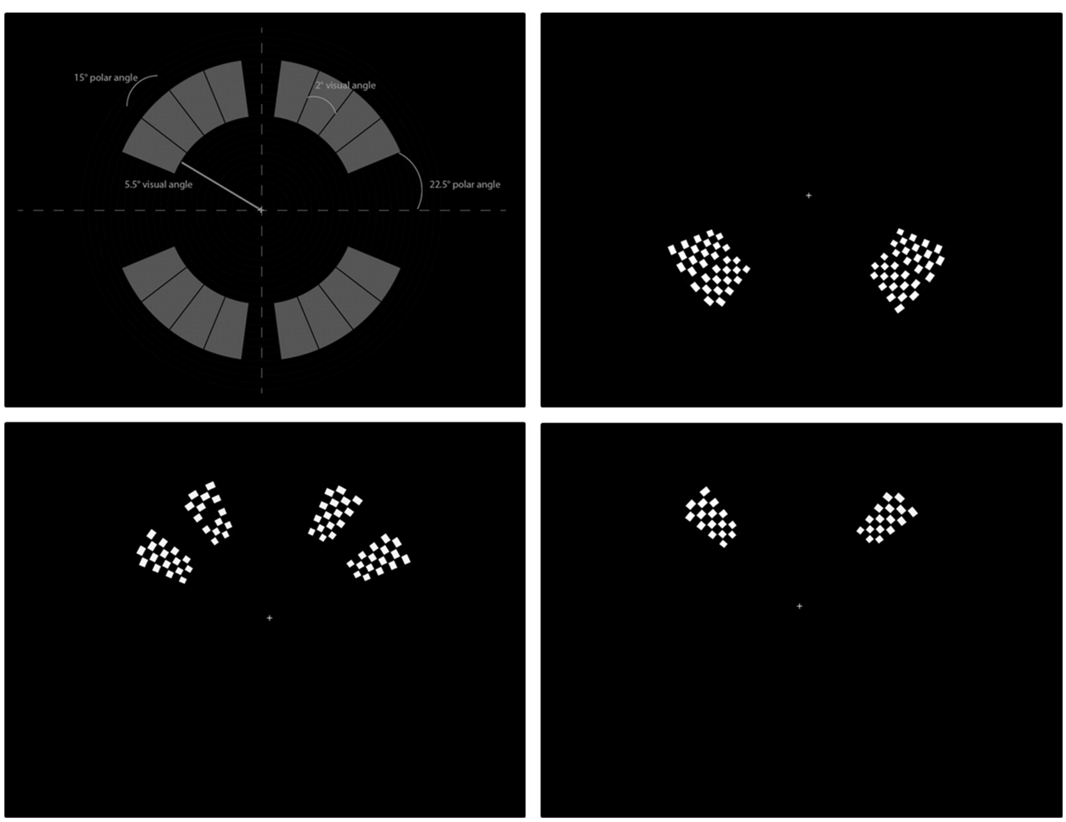

Fig. 1. Top left: Locations in which stimuli could be presented (grey segments) with measurements indicating size and position. Top right: Example of experimental screen layout for a dual-near target absent trial. In each trial type, the stimuli could be presented above or below fixation (each occurring on 50% of trials). Bottom left: Dual-far trial, with target present (upper left stimulus). Bottom right: Single stimulus target absent trial.