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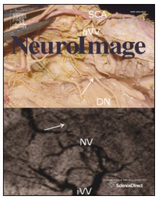

Visual, auditory and tactile stimuli compete for early sensory processing capacities within but not between senses

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ABSTRACT

We investigated whether unattended visual, auditory and tactile stimuli compete for capacity-limited early sensory processing across senses. In three experiments, we probed competitive audio-visual, visuo-tactile and audio-tactile stimulus interactions. To this end, continuous visual, auditory and tactile stimulus streams ('reference' stimuli) were frequency-tagged to elicit steady-state responses (SSRs). These electrophysiological oscillatory brain responses indexed ongoing stimulus processing in corresponding senses. To induce competition, we introduced transient frequency-tagged stimuli in same and/or different senses ('competitors') during reference presentation. Participants performed a separate visual discrimination task at central fixation to control for attentional biases of sensory processing. A comparison of reference-driven SSR amplitudes between competitor-present and competitor-absent periods revealed reduced amplitudes when a competitor was presented in the same sensory modality as the reference. Reduced amplitudes indicated the competitor's suppressive influence on reference stimulus processing. Crucially, no such suppression was found when a competitor was presented in a different than the reference modality. These results strongly suggest that early sensory competition is exclusively modality-specific and does not extend across senses. We discuss consequences of these findings for modeling the neural mechanisms underlying intermodal attention.

Introduction

Imagine standing in a particularly crowded place while listening to someone on your phone. People are walking all over the place; talking out loud; perhaps even bumping into you. You will have to try hard to focus on the caller's voice. This situation illustrates how in everyday life limited neural processing capacities force the human brain to actively select a specific source of information among a manifold of unrelated sensory events (Broadbent, 1952; Kastner and Ungerleider, 2000; Neisser and Becklen, 1975). In our example a distinction can be made between selecting the voice over background noise – a selection *within* the auditory modality – and selecting auditory information over visual and tactile information – a selection *between* sensory modalities. Q4 Q3

The neural mechanisms underlying attentional selection within a sensory modality have been formalized in the *biased competition* model (Kastner et al., 1998; Moran and Desimone, 1985). *Biased competition* rests on two central assumptions: (I) Two or more concurrent stimuli enter a competition for limited processing capacity that leads to mutual suppression. Although primarily established in visual attention research, modality-specific inter-stimulus competition can also be inferred from findings of suppressive effects between auditory (Kawase et al., 2012; Ross et al., 2012) and tactile stimuli (Severens et al., 2010). (II) Selective attention to one stimulus releases it from mutual suppression and biases the competition in favor of the selected stimulus' processing. Following these assumptions, inter-stimulus competition poses a necessary prerequisite for the attentional bias in modality-specific sensory processing.

Attentional selection between sensory modalities, i.e. 'intermodal' attention (Alho et al., 1992; Boulter, 1977; Eimer and Schröger, 1998; Porcu et al., 2013), is less well understood. It stands to question, whether the attentional mechanisms that constitute the biased competition framework also account for intermodal attention. Recent neuroimaging studies have investigated crossmodal[2] interactions in early sensory processing while participants attended to one sensory modality (Johnson and Zatorre, 2005; Langner et al., 2011; Laurienti et al., 2002; Shomstein and Yantis, 2004). A consistent finding of these studies was that neural activity that corresponded to the processing of input from unattended modalities decreased. This reduction might have been the consequence

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[2] The terms *intermodal* and *crossmodal* are sometimes used interchangeably in the literature to reference attention-related influences on multisensory processing. Here, we use *intermodal* to circumscribe higher order processes that control attentional allocation in modality-specific early sensory processing according to actual task demands. The term *crossmodal*, in turn, is used to reference low-level stimulus-driven influences that may occur task-independently.

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of a reallocation of processing capacities from unattended to attended sensory modalities. Importantly, such a push–pull mechanism necessarily implies (I) that sensory modalities share common processing capacities and (II) that sensory modalities compete for these common capacities.

However, in the studies described above, participants always attended to stimulation in at least one sensory modality. These situations must have imposed a strong bias on any crossmodal competition when we assume that a biased-competition-like mechanism governs intermodal attention. Participants' attention to visual stimulation, for example, imposed a strong bias towards visual processing while suppressing auditory and/or tactile processing. As a consequence, it has not been addressed to date whether (and how) visual, auditory and tactile processing interacts when neither stimulation is attended. An unbiased crossmodal competition that influences sensory stimulus processing per se has yet to be observed. As laid out above, such crossmodal competitive stimulus interactions would be the vital foundations of a biased-competition-like account of intermodal attention.

The present study aimed to test for crossmodal competition in the absence of an attentional bias. To this end, we conducted three experiments, all employing similar paradigms, yet, each featuring a unique combination of stimuli from two sensory modalities: visual and auditory stimuli in Experiment 1, visual and tactile stimuli in Experiment 2 and tactile and auditory stimuli in Experiment 3. In each experiment we frequency-tagged sensory stimulus streams ('reference stimuli') that were presented for several seconds. Frequency-tagged stimuli elicited oscillatory brain responses, phase-locked to stimulation that indexed the ongoing sensory processing in corresponding sensory modalities. These so-called steady-state responses (SSRs; Regan, 1989) have been shown to decrease in amplitude when a competing stimulus was presented in the same sensory modality in vision (Fuchs et al., 2008; Keitel et al., 2010), audition (Kawase et al., 2012; Ross et al., 2012) and touch (Severens et al., 2010). During reference stimulus presentation, we therefore introduced frequency-tagged 'competitors', i.e. stimuli of the same and/or different sensory modality, to induce competition. We compared amplitude changes of reference-driven SSRs between competitor-absent and competitor-present periods.

In all three experiments, participants were engaged in a visual discrimination task at central fixation. Participants were instructed to count brief contractions of the fixation cross while ignoring elongations. The task was designed to withdraw participant's attention from task-irrelevant peripheral visual, auditory and tactile reference stimuli and competitors in order to prevent attentional biases of inter-stimulus competition.

We hypothesized that, if, on the one hand, stimuli of different sensory modalities entered a crossmodal competition we would observe effects of suppression. SSR amplitudes during the competitor-present period would be lower than during the competitor-absent period. On the other hand, if no suppression occurred, SSR amplitudes would remain constant. Additionally, in line with previous studies on intramodal competition, we expected reduced SSR amplitudes during competitor-present periods to indicate suppression between stimuli within senses.

Consistently, across all combinations of stimuli, we found that suppression only occurred between stimuli of the same sensory modality but not between stimuli of different sensory modalities. Therefore, while well in line with biased competition governing processing within senses, our results challenge the notion of a biased competition for common processing capacities between senses.

General methods

Participants

Participants gave informed written consent prior to experiments. None reported a history of neurological diseases or injury. The experiments were conducted in accordance with the Declaration of Helsinki and the guidelines of the ethics committee of the University of Leipzig.

Stimuli

In each of the three experiments stimuli from two sensory modalities were presented. Experiment 1 employed visual and auditory stimuli. Experiment 2 featured the presentation of visual and tactile stimuli. In Experiment 3, we presented auditory and tactile stimuli. Detailed descriptions of stimuli are given below (see respective Methods sections).

Experimental procedure and task

Participants were seated comfortably in an acoustically dampened and electromagnetically shielded chamber in front of a 19 in. cathode ray tube (CRT) screen. The screen was set to a refresh rate of 120 frames per second and a resolution of 800 × 600 pixels (width × height). A white fixation cross (0.64° of visual angle in width and height, luminance = 110 cd/m^2) was presented in the center of the screen at a viewing distance of 80 cm. Participants were instructed to fixate the cross and to perform a demanding task, namely to discriminate between brief changes in length of one of the two bars of the fixation cross. Length increased or decreased by 20, 40 or 60%. These changes lasted 8 frames (67 ms) and occurred up to three times in every trial with a minimum interval of 600 ms between subsequent onsets. Participants had to count contractions in either one of the beams (= targets). Corresponding elongations had to be ignored (= distracters). Responses were given after each trial by pressing one of four buttons indicating zero, one, two or three counted targets. Response button layout was reassigned randomly for each trial to control for effects of motor preparation during trials.

All experiments formed full-factorial designs with two factors: In each trial, the reference stimulus was presented in one of two sensory modalities (factor *reference modality*). Additionally, a competitor was presented either in the same sensory modality as the reference stimulus, in the second sensory modality or competitors from both sensory modalities were presented in combination (factor *competitor modality*). For example, the first experiment investigated audio-visual stimulus interactions. Thus, in one half of all trials we presented a visual reference stimulus. In the other half we presented an auditory reference stimulus. Both stimuli could either be paired with a visual, an auditory or a combined audio-visual competitor yielding a total of six experimental conditions.

In each experiment, we presented 420 trials divided into 6 blocks of 70 trials each (~5 min duration) with trials of all six conditions intermingled randomly across blocks. Participants started blocks by a button press. Prior to the experiment, they performed a short training session of at least one block (~5 min). After each training and experimental block, they received feedback about their average correct-response rate.

As illustrated in Fig. 1A, each trial began with the presentation of the fixation cross for 800 ms followed by the onset of the reference stimulus, which was presented for 3000 ms. Competitor presentation started with a randomly chosen lag of 200 or 400 ms after reference stimulus onset. Both stimuli were presented simultaneously for a randomly chosen interval of 1200, 1400 or 1600 ms (see Fig. 1B). After competitor offset, the reference stimulus remained presented until trials ended.

Task-relevant changes of the fixation cross only occurred during the presentation of reference stimuli in the presence and absence of competitors. At the end of each trial, the fixation cross was replaced by a graphical scheme of the current button layout for 1700 ms prompting participants for a response (see Fig. 1 for a trial schematic). Additionally, participants were instructed to blink during the response prompt period to minimize eye movements during trials. The target count in corresponding trials was considered incorrect when participants missed to press a button. Any button press started the next trial immediately.

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