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Proprioceptive cues modulate further processing of spatially congruent auditory information. A high-density EEG study

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Abstract

Multisensory integration and interaction occur when bimodal stimuli are presented as either spatially congruent or incongruent, but temporally coincident. We investigated whether proprioceptive cues interact with auditory attention to one of two sound sources in free-field. The participant's task was to attend to either the left or right speaker and to respond to occasional increased-bandwidth targets via a footswitch. We recorded high-density EEG in three experimental conditions: the participants either held the speakers in their hands (Hold), reached out close to them (Reach), or had their hands in their lap (Lap). In the last two conditions, the auditory event-related potentials (ERPs) revealed a prominent negativity around 200 ms post-stimulus (N2 wave) over fronto-central areas, which is a reliable index of further processing of spatial stimulus features in free-field. The N2 wave was markedly attenuated in the 'Hold' condition, which suggests that proprioceptive cues apparently solidify spatial information computed by the auditory system, in so doing alleviating the need for further processing of spatial coordinates solely based on auditory information.

Keywords

Event-related potentials (ERPs); auditory; proprioceptive; crossmodal; attention

1. INTRODUCTION

Inputs arriving at primary sensory areas from different modalities have to be integrated to produce a partially redundant but consistent internal representation of the world (Driver & Spence, 1998). Early groundbreaking animal studies in cats demonstrated that multisensory facilitation requires spatial congruity between stimuli from different modalities (Stein & Meredith, 1993; Stein, 1998). These authors reported that cells in the superior colliculus and other cortical association areas exhibited super-additive activity to concurrent bimodal stimulation as long as stimuli from two different modalities appeared in close spatial proximity. Typically, spatially congruent bimodal stimuli are responded to faster and more accurately than

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We found a significant difference in the amplitudes of the P3 elicited by attended and unattended deviants ($F[1,11] = 48.09, p < .0001$), which confirmed that our attentional manipulations was effective, i.e., deviants in the unattended channel hardly elicited any positivity during the latency range of the P3 wave. No significant differences were found for P3 amplitudes elicited by attended target stimuli across the three experimental conditions ($F[2,10] = 2.02, n.s., p = .15$). Since the P3 wave was not sensitive to our experimental manipulations, we did not analyze it further.

when being presented unimodally (Frassinetti, Bolognini, & Ládavas, 2002; Frens, Van Opstal, & Van der Willigen, 1995).

However, we also know that some facilitatory cross-modal interactions do not depend upon spatial coincidence *per se* as long as the temporal coincidence of bimodal stimuli is not critically violated (Stein, London, Wilkinson, & Price, 1996; Teder-Sälejärvi, Di Russo, McDonald, & Hillyard, 2005). A recent study reported that auditory-somatosensory interactions share the same sensory mechanisms independent of whether these bimodal stimuli are in spatial register or not (Murray, Molholm, Michel, Heslenfeld, Ritter, Javitt, Schroeder, & Foxe, 2005). In this study, reaction times were significantly facilitated when participants were presented with concurrent somatosensory and auditory stimulation even when they originated from different spatial locations.

Findings regarding multisensory processing when the own body is implicated convincingly illustrate the multi-faceted task the brain engages in when dovetailing converging sensory data into meaningful representations. For example, orienting the eyes to a body site facilitates somatosensory processing (Larmande & Cambier, 1981; Pierson, Bradshaw, Meyer, Howard, & Bradshaw, 1991; Taylor-Clarke, Kennett, & Haggard, 2002); this even holds true in complete darkness (Tipper, Lloyd, Shorland, Dancer, Howard, & McGlone, 1998, Driver & Grossenbacher, 1996; Honoré, Bourdeaud'hui, & Sparrow, 1989).

From monkey studies it is known that the premotor cortex integrates proprioceptive, visual, and tactile information. Some neurons appear to have a visual receptive field in proximity to the arm that does not move with the eyes, is not anchored in retino-centric coordinates, but rather follows through extra-personal space in rough correspondence with the position of the arm (Graziano & Gross, 1998; Graziano, 1999).

Further, tool use by monkeys and humans is known to cause reorganization or visuo-tactile limb representations, such that receptive fields will expand to involve the tools extending from the hands (Johnson-Frey, 2003, 2004). If tools can induce this sort of functional reorganization in visuo-tactile representations, it seems likely that informative auditory cues will aid to form the representation of extrapersonal space. Indeed, in a study investigating audio-tactile interactions, human participants showed performance decrements to electro-cutaneous target stimuli delivered to the earlobes when auditory distracters were presented on the opposite side behind the head (Kitagawa, Zampini, & Spence, 2005).

The goal of the present study was to investigate whether proprioceptive cues interact with auditory attention using a robust sustained-attention paradigm. Specifically, we were interested whether the position of the participant's hands in *peri-personal* space has an influence on auditory stimulus processing since it has been shown in a variety of species that stimuli from different sensory modalities are integrated in a limited space surrounding the body (Rizzolatti, Fadiga, Fogassi, & Gallese, 1997). Participants attended to a left or right speaker and responded to occasional "deviant" increased-bandwidth targets via a footswitch. The participants either rested their hands in their laps (LAP), reached out next to the speakers without touching them (REACH), or held the speakers in their hands (HOLD).

2. RESULTS

Behavioral data

Participants were on the average 83% accurate in responding to attended target deviants across all conditions. As shown in Figure 1, accuracy did not vary significantly between conditions ($F[2,10] = 1.98$, n.s., $p = .16$). False alarm rates were not analyzed due to their low occurrence rate (.31%). There was a significant difference in reaction times (RTs) between conditions (F

[2,10] = 4.95, $p < .02$). Although the individual contrast tests were not significant as revealed by Bonferroni post-hoc comparisons, this effect was apparently driven by faster RTs in the Lap condition compared to both Reach and Hold conditions.

ERP data

In the present fast-paced auditory oddball paradigm, attended and unattended stimuli elicited ERPs with a well known morphology. We observed a classic bi-phasic attention effect with an early phase around the latency of the auditory N1 wave and a later phase at the latency of the N2 deflection. This well-established attention effect is called “processing negativity” (Näätänen, 1982; Teder, Alho, Reinikainen, & Näätänen, 1993), has also been termed Nd for “negative difference wave (Hansen & Hillyard, 1988), and reflects preferential processing of attended stimulus features and is best visualized in a difference wave. We prefer to show ERPs to attended stimuli, because the Nd measure requires subtraction of ERPs taken under two different experimental conditions.

A prominent P1 wave was observed with a frontocentral peak latency of 86 ms post-stimulus which was not systematically modulated by attention (*attention* $\times$ *location* interaction, ($F[1,11] = 3.66$, n.s., $p = .08$) and did not differ in amplitude across conditions ($F[2,10] = .41$, n.s., $p = .57$). The earliest effect of attention was observed between 100–150 ms post-stimulus, the typical latency range of the fronto-central N1 wave which indexes early sensory processing, i.e., feature encoding. The attention effect is defined as the amplitude difference between the attended and unattended ERPs (see Figure 2). A repeated-measures ANOVA revealed that the effect of attention was indeed significant, ERPs to attended stimuli had larger amplitudes in all three experimental conditions ($F[1,11] = 17.15$, $p < .002$). There was also a significant *location* $\times$ *cluster* interaction confirming that the N1 amplitudes were consistently larger contralateral to the stimulated side ($F[2,10] = 21.41$, $p < .0001$).

During a latency range of 240–280 ms we observed a prominent negative deflection, the so-called N2. This waveform has been implicated to reflect the neural underpinnings of categorization mechanisms and elaborated further processing of attended stimulus features (Teder, Alho, Reinikainen, and Näätänen, 1993; see Figure 3.)

In contrast to the contra-lateral distribution of the N1, the N2 had a more broad fronto-central scalp topography without any signs of laterality (*location* $\times$ *cluster* interaction, $F[1,11] = 2.79$, n.s., $p = .09$). The mean amplitude of the N2 was significantly different between experimental conditions during the time range of 240–280 ms ($F[1,11] = 5.16$, $p < .02$). Bonferroni post-hoc comparisons confirmed that attended N2 amplitudes in the Hold condition were significantly reduced in comparison to Lap ($t[11] = 6.53$, $p < .03$) and Reach ($t[11] = 5.65$, $p < .04$) conditions (see Figure 4). However, there were no significant differences in N2 amplitudes between Lap and Reach conditions ($t[11] = .33$, $p > .57$).

3. DISCUSSION

Behavioral data

Response accuracy did not differ systematically across conditions, but RTs were faster in the Lap condition. We speculate that this might be due to the fact that in the Reach and Hold conditions, participants were involved in two concurrent motor tasks (i.e., stretching the arms out towards the speakers while at the same time pushing the footswitch in response to the targets). Conversely, in the Lap condition participants only had to perform one motor task, namely pressing the footswitch to targets.

Electrophysiological data

The ERPs elicited by the auditory stimuli used in this study showed a typical and well-established morphology: The P1 wave was present in unattended and attended ERPs and did not show any signs of attentional manipulation which replicates previous findings using a very similar experimental paradigm in free-field (Teder & Näätänen, 1994; Teder-Sälejärvi & Hillyard, 1998; Teder-Sälejärvi, Hillyard, Röder, & Neville, 1999).

The N1 wave has multiple bilateral generators in the primary and secondary auditory cortices, and a non-specific component probably generated in the frontal motor and premotor cortex (Näätänen & Picton, 1987). This waveform indexes early stimulus processing such as encoding physical stimulus features and was similarly modulated by attention in all three experimental conditions. No statistically significant differences were found.

The N2 is a well-known index of further processing and categorization of incoming stimuli, and is reliably elicited when competing spatial locations in free-field require a rather difficult discrimination (Näätänen, 1992; Teder et al., 1993; Teder & Näätänen, 1994; Teder-Sälejärvi & Hillyard, 1998; Teder-Sälejärvi et al., 1999).

The present findings show that when participants are in physical contact with the source of an auditory stimulus (Hold), thus utilizing corroborating spatial information derived from proprioceptive cues, the N2 wave is significantly attenuated as compared to when their hands are near to (Reach), or far away from (Lap), the sound source. The profound attenuation of this waveform suggests that further processing of a spatial location based on auditory information is apparently not taking place since participants are aware of the locations of their hands in extra-personal space even when they are not directly visible.

These results come as no surprise since previous studies have partially elucidated the neural underpinnings of the body image involved in tool use (for review, see Johnson-Frey, 2003, 2004). From monkey studies, we know that somatosensory and visual stimuli are integrated in the premotor and parietal cortex (Maravita & Iriki, 2004; Hihara, Notoya, Tanaka, Ichinose, Ojima, Obayashi, Fujii, & Iriki, 2006; Obayashi, Suhara, Kawabe, Okauchi, Maeda, Akine, Onoe, & Iriki, 2001). Maravita and colleagues (2004) found so-called bimodal neurons which responded to somatosensory stimuli at the hand, and to visual stimuli near the hand. However, one of their crucial findings was that the receptive fields of these bimodal neurons expanded after brief training of the monkey such that the entire tool was included. We also know of neurons in the premotor cortex that respond to the felt position of the arm when it is covered from direct view but also respond to images of a fake arm (Graziano, 1999). Homologous circuits in humans have been demonstrated in human participants using neuro-imaging techniques (Culham & Kanwisher, 2001). Reaching with a tool does in fact extend cross-modal, visual-tactile interactions into extrapersonal space (Maravita, Husain, Clarke, & Driver, 2001), and participants show behavioral facilitation when responding with the lift of a finger to a red laser dot when it appears directly upon the finger tip as opposed to when it appears next to it (Hari & Jousmäki, 1996). Similar facilitatory interactions between the auditory and tactile senses were also reported in a psychophysical study by Schürmann, Caetano, Jousmäki, & Hari (2004). Behavioral and neural facilitation has been demonstrated in human participants when audio-visual stimuli were presented in spatial register (Teder-Sälejärvi et al., 2005), and when an auditory stimulus was delivered at the same time as a vibrotactile stimulus to the fingers, even when the speaker delivering the tone was located near the opposite hand (Murray et al., 2005). Further, auditory distracters behind the head slowed responses to spatially incongruent vibro-tactile stimulation of the earlobes (Kitagawa et al., 2005).

A growing body of evidence suggests that the functional significance of neural networks maintaining and updating body shape and posture in reference to the locations of objects in

extra-personal space is to provide converging multi-modal information determining subsequent behavior. The present results speak to situations in which integration of audio-tactile information is of paramount importance in creating a veridical representation of the world. Specifically, when individuals must function in the dark (Graziano, Hu, & Gross, 1997), and when events are occurring outside of their visual field (Graziano, 1999), multimodal redundancy helps to guide and refine efficient actions. Our results suggest that physical contact with a sound source appears to give participants a neural advantage when solidifying the spatial location of a sound source in free-field, i.e., holding a speaker in your hand makes further processing based on auditory cues obsolete. Future experiments with densely spaced speaker arrays will have to address the effects of auditory stimuli in close proximity to the hands in peri-personal space.

4. EXPERIMENTAL PROCEDURE

Subjects

Twelve subjects (five women; ages 18–32 years, mean age 23.2 years) participated in this experiment after giving written informed consent, 11 of the participants were right-handed. All of the participants had normal or corrected-to-normal vision and were tested in the laboratory to confirm normal hearing. All participants completed a health survey and had no history of neurological problems. Participants were either paid volunteers or university students who completed the study for class credits and were recruited through the online subject pool at North Dakota State University. Paid participants were reimbursed \$8/hour for study participation. The experiment was performed with the approval of the North Dakota State University Institutional Review Board for the protection of human participants in research.

Experimental setup

The subjects were seated in a dimly lit electrically and magnetically shielded chamber. Participants sat on a raised stool while experimenters placed the electrode cap on their heads. Electrode gel was applied to each electrode location and then the electrodes were plugged into the cap. Impedances at all electrode sites were checked and kept below 5 kOhms. Participants were then moved to a comfortable chair and the lights in the room were dimmed. In order to minimize blinks and eye-movements, participants were instructed to keep their gaze on a central fixation point throughout each experimental block, and to press a foot pedal in response to infrequent target stimuli (accuracy was emphasized over speed. Participants' gaze was monitored via a camera mounted on the wall and focused on their face.

Participants completed 12 experimental blocks (4 for Lap, Reach, and Hold each, divided between attend right and attend left conditions), each lasting 3.5 minutes in length, and were encouraged to break and rest their eyes in between blocks. During each break between blocks, experimenters instructed participants over a loudspeaker from the experimental chamber on decreasing eye blinks and eye movements in order to ensure clean data. The net recording time for the entire experiment was 42 minutes in length, and the entire experiment took approximately an hour to complete including breaks and instructions. Once participants had completed the experiment, the electrode cap was removed and they were debriefed as to the purpose of the study.

Stimuli and Apparatus

A fast-paced random sequence of pink noise bursts (50 ms duration, @76 dB SPL) was delivered by two small enclosed loudspeakers (left/right, 60° apart, at 60 cm distance, i.e., an arm-length from the participant); the participant's task was to attend to either the left or right speaker and to respond to occasional increased-bandwidth targets from the attended speaker via a footswitch. The target stimuli occurred 5% of the time, such that frequent "standard"

stimuli occurred 47.5% of the time from each speaker, and targets occurred 2.5% of the time from each speaker. Participants were instructed to ignore all stimuli emanating from the unattended speaker. A random sequence of stimuli was presented with an inter-stimulus interval (ISI) of 120–360 ms (rectangular distribution). The participants either held the speakers in their hands (Hold), reached out to the speakers at the same distance (Reach), or had their hands in their lap (Lap). In the Hold condition, participants cupped their hands around the sides of the speakers so that their palms were in direct contact with the speakers during the experimental block. It was confirmed in pilot runs that no vibrations were being delivered to participants' palms through the speakers during auditory stimulation in this condition. In the Reach condition, participants placed their hands to either side of the speakers, with their palms down on the table, and no physical contact was made with the speakers. In the Lap condition, participants kept their hands resting in a comfortable position in their laps. Other than these differences, the task requirements and instructions did not vary across conditions.

Behavioral data

The percentage of correct target detections (Hits) and mean reaction times (RTs) were calculated for each of the stimulus conditions (attended left and right targets across Lap, Reach, and Hold). False Alarms were defined as a response to any stimulus that was not an attended target. A response was associated with a preceding target if it occurred between 200 and 800 ms after target onset, other responses falling outside this window were discarded and classified as false alarms. The stimulus sequences were edited such that no two targets ever occurred in succession so that hits could be accurately calculated using this algorithm. In order to examine potential differences in accuracy and RT between experimental conditions, a two-way within-subjects ANOVA was run with the factors of *condition* (Lap, Reach, Hold) and *location* (Left or Right). Due to the low percentage of False Alarms (.31%), statistical tests were not performed on these data.

ERP recordings

The EEG was recorded from 162 scalp sites with an ActiveTwo BioSemi electric system (<http://www.biosemi.com>; Biosemi, Amsterdam, the Netherlands) and the EOG was monitored with a total of six electrodes located at the outer canthi and above and under each eye, respectively. The sampling frequency was 512 Hz, with a pass-band from DC to 150 Hz. During recording, Biosemi replaces the “ground” electrodes which are used in conventional systems with two separate electrodes: the “Common Mode Sense” active electrode and the “Driven-Right-Leg” passive electrode. A description of grounding and referencing conventions used by the BioSemi system during recording can be found at: <http://www.biosemi.com/faq/cms&drl.htm>. Once the data is acquired, any electrode or combination of electrodes can be assigned as “reference”; we chose to rereference off-line to the averaged mastoids.

The data were analyzed using BESA version 5.1.8 (Brain Electric Source Analysis, Gräefelfing, Germany). Automated artifact rejection was performed prior to averaging to discard trials during which an eye movement, blink, or amplifier blocking occurred. Artifact criteria of $\pm 120 \mu\text{V}$ from -100 to 500 milliseconds of stimulus onset were applied, and the data were also visually inspected for blinks and eye movements. The remaining trials were then averaged per condition, with a baseline of -100 to 0 ms. For analysis and display purposes, data were filtered with a 0-phase-shift 35 Hz fourth-order Bessel low-pass filter (fall-off: 24 dB/octave). No high-pass filtering was applied to the data.

Data analysis

For statistical testing, analyses of variance (ANOVAs) were carried out comparing mean amplitudes within specified time windows centered to the peak deflections of interest

referenced to the 100 ms pre-stimulus baseline. The following time windows were tested: 60–110 ms (P1 wave), 125–145 ms (N1 wave), 240–280 ms (N2 wave), and 350–450 ms (P3 wave).

For all time windows, amplitudes were measured at 26 sites in three clusters: a left and right cluster of ten electrodes per hemisphere, and a central cluster of six electrodes (fronto-central mid-line). These fronto-central sites for the left cluster extended from electrodes approximating F1 to F3 and down to C1 and C3 in the 10-10 system, and from F2 to F4 and down to C2 and C4 for the right cluster. The central cluster extended from Fz to Cz in the 10-10 system.

In order to examine the “attention affect” (attended ERPs minus unattended ERPs) during the P1 and N1 latency range, as well as to probe for differences across conditions, mean ERP amplitudes of frequent attended and unattended “standard” stimuli were subjected to a repeated-measures ANOVA with the factors *condition* (Lap, Reach, Hold), *location* (left or right), *attention* (left or right) and *cluster* (left, right, center). The statistical testing for mean amplitude differences across conditions at the N2 latency was performed in the same way on the attended standards with the factors *condition*, *location*, and *cluster*.

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Figure 1. The left panel shows average hit rates across subjects ($n=12$) for each experimental condition. The right panel depicts reaction times to infrequent target stimuli at the attended location. The error bars represent the standard error of the mean (SEM).

Figure 2.

Unattended and attended grand-average ERPs across the three experimental conditions over three fronto-central sites approximating the locations of FC3, FCz, and FC4 in the 10-10 system. The center panel shows the experimental conditions, the participants either had their hands close to their body (Lap), reached out close to the speakers (Reach), or held the speakers in their hands (Hold). The time range for the iso-potential topographical maps is 130–150 ms.

Figure 3.

Attended grand-average ERPs across the three experimental conditions over five fronto-central sites approximating the locations of FC3, FC1, FCz, FC2, and FC4 in the 10-10 system. The time range for the iso-potential topographical maps is 240–280 ms.

Figure 4. Mean amplitudes of the attended grand-average N2 deflection (240–280 ms) across the three experimental conditions. The error bars represent the standard error of the mean (SEM).