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Location-independent and location-linked representations of sound objects

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ABSTRACT

For the recognition of sounds to benefit perception and action, their neural representations should also encode their current spatial position and their changes in position over time. The dual-stream model of auditory processing postulates separate (albeit interacting) processing streams for sound meaning and for sound location. Using a repetition priming paradigm in conjunction with distributed source modeling of auditory evoked potentials, we determined how individual sound objects are represented within these streams. Changes in perceived location were induced by interaural intensity differences, and sound location was either held constant or shifted across initial and repeated presentations (from one hemispace to the other in the main experiment or between locations within the right hemispace in a follow-up experiment). Location-linked representations were characterized by differences in priming effects between pairs presented to the same vs. different simulated lateralizations. These effects were significant at 20–39 ms post-stimulus onset within a cluster on the posterior part of the left superior and middle temporal gyri; and at 143–162 ms within a cluster on the left inferior and middle frontal gyri. Location-independent representations were characterized by a difference between initial and repeated presentations, independently of whether or not their simulated lateralization was held constant across repetitions. This effect was significant at 42–63 ms within three clusters on the right temporo-frontal region; and at 165–215 ms in a large cluster on the left temporo-parietal convexity. Our results reveal two varieties of representations of sound objects within the ventral/What stream: one location-independent, as initially postulated in the dual-stream model, and the other location-linked.

Introduction

Today's view of auditory processing is very much influenced by the dual-stream model (Rauschecker and Scott, 2009), which is derived from electrophysiological studies in non-human primates (Kaas and Hackett, 2000; Rauschecker and Tian, 2000) as well as from activation (Alain et al., 2001; De Santis et al., 2007; Maeder et al., 2001) and lesion studies in humans (Clarke et al., 2000, 2002). Its basic tenet, segregation of auditory processing between the ventral/What stream, leading ultimately to the identification of a sound object, and the dorsal/Where stream, leading to its localization, is well supported by several lines of evidence. The dorsal/Where stream has been shown to be involved in different aspects of auditory spatial processing (Arnott et al., 2004), including the refinement of auditory spatial representations associated with training-induced improvement in discrimination (Spierer et al., 2007a, 2011) and the explicit judgment of sound positions (as demonstrated by transcranial magnetic stimulation: At et al., 2011; Lewald et al., 2004). Neural activity within the ventral/What stream codes for environmental sound objects (De Lucia et al., 2010a; Murray et al., 2006) and exhibits repetition-induced priming effects, which have been reported with two types of paradigms. First, a series of studies described a decrease in neural responses to repeated vs. initial stimulus presentations that were themselves separated by intervening stimuli or by separate study and test sessions (Bergerbest et al., 2004; Bourquin et al., 2012; De Lucia et al., 2010b; Murray et al., 2008). Repetition priming effects usually manifest as suppression but sometimes as enhancement (Henson et al., 2000); depending on parameters that are currently unclear. Second, other studies used an adaptation paradigm, with initial and repeated presentations paired together in (nearly) immediate succession (e.g. Altmann et al., 2008a, 2008b, 2010; Doehrmann et al., 2008). The underlying rationale is that the recovery from an adapted level of responsiveness reveals sensitivity to a given stimulus or cognitive dimension (Grill-Spector and Malach, 2001). One advantage conferred by the first type of paradigm, where initial and repeated presentations are separated by intervening stimuli, is that repetition-related effects can be dissociated more readily from habituation to low-level stimulus features. Furthermore, several previous auditory evoked potential studies used this approach successfully to investigate repetition priming effects within sound object representations (Bourquin et al., 2012; Murray et al., 2008) and their further use will allow more readily for a synthesis of findings.

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It is likewise worth noting that the overwhelming majority of these previous studies examining repetition-induced plasticity in sound representations concentrated on semantic (and not spatial) features of sound object representations and used centrally presented stimuli for primes and repeats. One exception is found in Altmann et al. (2008a) who investigated pattern vs. location changes with an fMRI adaptation paradigm. They found modulations for pattern changes within the ventral/What stream and modulations for location changes within the dorsal/Where stream.

Using the repetition priming paradigm the present study examined how the combined information of sound object identity and its location is represented within the auditory processing streams. The study was driven by the hypothesis that the human auditory cortex carries both location-independent and location-linked representations of sound objects. The former was expected to be characterized by repetition effects independent of the respective lateralizations of the prime and the repeat, and the latter to yield different repetition effects in pairs with the same vs. different lateralizations. Previous work, which did not vary the spatial location of stimuli across initial and repeated presentations, revealed priming effects at 156–216 ms post-stimulus onset within cortical regions known to be part of the ventral auditory stream, on the middle temporal gyrus and within the superior temporal sulcus on the left side (Murray et al., 2008); these effects were in terms of the global field power and not in terms of modulations in the topography of the auditory evoked potentials. These effects are believed to characterize a semantic, non-spatial representation of sound objects, but this hypothesis has never been actually tested. The existence of position-linked representations of sound objects is suspected on the basis of a recent 7T fMRI study; out of two early stage auditory areas known to be selective for sound recognition (as opposed to sound localization; Viceic et al., 2006), one was shown to be modulated by the position of environmental sounds, while the other was not (van der Zwaag et al., 2011). Results presented in this paper suggest that the auditory ventral/What pathway carries a dual representation of sound objects, one position-independent and the other position-linked.

Materials and methods

Main experiment

Subjects

Twelve right-handed male subjects (mean ± SD lateralization index = 84.08 ± 6.30; Oldfield, 1971) aged between 20–38 years (mean ± SD = 26.3 ± 5.5 years) participated in the study. None had a history of neurological or psychiatric illness, and all reported normal hearing. They provided written informed consent and were paid modestly for their participation in the experiment. This study was approved by the Ethics Committee of the Faculty of Biology and Medicine of the University of Lausanne.

Experimental procedures

Subjects listened to environmental sounds and classified them, as rapidly as possible, as produced by a living or manufactured source by pressing one of two buttons of a serial response box while continuous 160-channel EEG was recorded (detailed below). They performed a sound categorization task, which minimized the necessity to process spatial information for task completion. In this way, we could determine orthogonal influences of spatial information on object processing as well as repetition effects. Each of the 40 sound objects (20 from living: baby crying, bird, cat, coughing, chicken, clearing throat, cow, crow, dog, donkey, frog, gargling, laughter, owl, pig, rooster, scream, sheep, sneezing, and whistling; and 20 from manufactured sound sources: accordion, bicycle bell, car horn, cash register, church bell, cuckoo clock, doorbell, door closing, flute, glass shattering, guitar, harmonica, harp, organ, piano, police siren, saxophone, telephone, trumpet and violin; as already used by Murray et al., 2006) were presented twice (initial and repeated presentation) within a block after 0 to 5 other intervening sounds. The sounds were delivered through insert earphones (ER-4P; www.etymotic.com) at a sound pressure level of 88 dB to the ear receiving the more intense sound and 35 dB to the opposite ear 88 dB. This generated an intensity ratio of 72:28 and an IID of 8.2 dB, using the formula IID = 20log(72/28). As described in the follow-up study (see below), they were perceived at ca 65°. Similar IIDs were used in previous studies yielding lateralizations of similar angular values (e.g. Spierer et al., 2009; Tardif et al., 2006). Within each of the 16 blocks, sounds were presented with a pseudo-random inter-stimulus interval of 1600 ms to 2400 ms (in 100 ms steps). The lateralization of the initial and the repeated presentations of a given object within a block were either the same or different (same = S: R-R, L-L; different = D: R-L, L-R; the 4 possibilities each accounted for 25% of the pairs within a block and were mixed pseudo-randomly). The initial and the repeated presentations of a given sound object were either acoustically different exemplars of the same sound object (e.g. of the same dog barking) or identical exemplars. This was done to minimize cross-over effects across blocks (along with the use of a break between blocks; see also Murray et al., 2008 for a similar approach). The four possibilities accounted each for 25% of the pairs within a block and were pseudo-randomly distributed across the 16 blocks of the whole experiment. The relationship between the acoustic nature of the repeated exemplar (identical or not) and its position with respect to the initial presentation (same or different) was pseudo-randomized and balanced across sound objects and subjects. Because prior research has demonstrated equivalent priming and repetition suppression effects with both acoustically identical and different exemplars (De Lucia et al., 2010b), we reasoned that any effects linked to using identical vs. distinct exemplars would be counter-balanced across our factors of interest (i.e. same/different sound lateralization and initial/repeated presentation). Moreover, the repeats at the same lateralization and those at different lateralizations were equally often preceded by stimuli in the same or different position (Fig. 1) to avoid bias arising from spatial attentional priming induced by the preceding stimulus (Posner, 1980).

The time lag and the number of intervening items between the initial and repeated presentations of a given sound object ranged from 2 to 12 s (0 to 5 distinct intervening items, none of which were exemplars of the same auditory object) and they were kept constant across participants. In order to avoid systematic bias arising from order presentation across subjects, the presentation order of the blocks was determined by a Latin square design. The blocks were separated by six minute breaks, during which the participants were exposed to another kind of auditory stimuli (series of four pure tones) which were irrelevant to the experimental paradigm. This was in part done to allow sufficient time for an effective "resetting" of priming effects from one block to the next and therefore to minimize any carry-over effects from one block to the next (Murray et al., 2008). The whole experiment lasted approximately 2.2 h.

EEG recording and pre-processing

Continuous EEG was recorded at 1024 Hz through a 160-channel Biosemi ActiveTwo system (Biosemi, Amsterdam, Netherlands). EEG pre-processing and analyses were performed using Cartool (Brunet et al., 2011; http://sites.google.com/site/fbmlab/cartool). EEG epochs including 100 ms pre- to 500 ms post-stimulus onset were averaged, and auditory evoked potentials (AEPs) were calculated for the four experimental conditions: congruent and incongruent pairs; initial and repeated presentations. Trials with eye blinks or transient noise were rejected offline using a semi-automated ± 60 μV criterion at every channel as well as visual inspection of the raw EEG signals. The average number of accepted epochs was 269 ± 2 (mean ± standard deviation) for each of the four AEPs calculated per subject. For the analysis involving the collapsing of data across all initial presentations vs. all repeated presentations (irrespective of whether or not the perceived location