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ORIGINAL PAPER

Repetition-Induced Plasticity of Motor Representations of Action Sounds

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Abstract Action-related sounds are known to increase the excitability of motoneurones within the primary motor cortex (M1), but the role of this auditory input remains unclear. We investigated repetition priming-induced plasticity, which is characteristic of semantic representations, in M1 by applying transcranial magnetic stimulation pulses to the hand area. Motor evoked potentials (MEPs) were larger while subjects were listening to sounds related versus unrelated to manual actions. Repeated exposure to the same manual-action-related sound yielded a significant decrease in MEPs when right, hand area was stimulated; no repetition effect was observed for manual-action-unrelated sounds. The shared repetition priming characteristics suggest that auditory input to the right primary motor cortex is part of auditory semantic representations.

Keywords Priming · Repetition suppression · TMS · MEP · Action-related sound · Motor plasticity

Introduction

Apart from the well documented activations within auditory regions, environmental sounds related to actions were shown to co-activate parts of prefrontal, premotor and motor cortices bilaterally (Lahav et al. 2007; De Lucia et al. 2009) or predominantly on the left side (Lewis et al. 2005; Pizzamiglio et al. 2005; Gazzola et al. 2006; Hauk et al. 2006; Doehrmann et al. 2008). The specific involvement of the primary motor cortex was demonstrated by transcranial magnetic stimulation (TMS); motor evoked potentials (MEPs) to stimulation of the hand area were shown to be larger while subjects listened to manual-action-related than unrelated sounds (Aziz-Zadeh et al. 2004).

Repetition induced plasticity is a key feature of perceptual and semantic representations of objects; it occurs when a neuronal population encounters repeatedly stimulus features which it perceives as identical (Henson 2003; Grill-Spector et al. 2006). Repetition suppression, i.e. decrease of neural activity during repeated exposure, is characteristic of the core semantic representation of sound objects in the left temporal convexity (Bergerbest et al. 2004; Murray et al. 2008; De Lucia et al. 2010; Bourquin et al. 2012) and of category specific representation in the left and right supratemporal plane and superior temporal gyrus (Doehrmann et al. 2008). If the auditory input to the primary motor cortex is part of the semantic representation of action-related sounds, it is likely to share its repetition priming features, including at the level of the motor output of the primary motor cortex. We tested this hypothesis by applying TMS to the hand area and comparing MEPs, which were recorded from the first dorsal interosseus muscle (FDI) while the subjects were listening to initial versus repeated presentations of manual-action-related or unrelated sounds.

Materials and Methods

Eighteen right-handed (mean ± SD = 89.17 ± 14.58; Oldfield 1971) volunteers (12 females) aged between 19–26 years (mean ± SD = 23.2 ± 2.3 years) participated in the study. None had a history of neurological or psychiatric illness, and all reported normal hearing.

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Participants provided written informed consent and were moderately remunerated for their participation. All procedures were approved by the Ethics Committee of the Faculty of Biology and Medicine at the University of Lausanne.

The stimuli were 60 environmental sounds of which 30 were related to manual actions (M+) and 30 were not (M−). The category M+ included 10 sounds related to unimanual (clinking glasses; brushing; hooting; knocking on a door; filling up a glass with a liquid; leafing through a book; spraying; dialing a phone number; ringing a bicycle bell; slapping), 10 to bimanual (playing the accordion, harp, piano, violin, drum, tambourine; typing; using the pneumatic drill; clapping hands; sharpening a knife), and 10 to hand–face actions (playing the recorder, flute, bagpipes, trumpet; brushing teeth; coughing; Native American war cry; whistling; hissing; shaving). The category M− included 10 sounds related to face (snoring; crying baby; and saying: [o], [di], [Zy], [la], [ni], [vA], [ga], and [Zi]), and 10 to leg actions (running; tap dancing; steps on different floor material: two types of gravel, flagstone, tiled floor, two types of wooden floor, resonant courtyard, and two kind of street steps), while 10 were unrelated to immediate human action (a plane; cricket; helicopter; clock; storm; hens; wind; dog; train; fire). These sounds were 4 s in duration, including a 50 ms linear raise and fall time; (16 bit stereo; 22.5 kHz digitization) and were normalized according to the root mean square of their amplitude. They were presented at an intensity of 80 ± 3 dB through insert earphones (ER–4P; www.etymotic.com). Each sound was followed by a 3 s silent interval. The capacity of the subject to recognize the sounds was evaluated prior to the TMS experiment. The TMS experiment comprised 4 experimental blocks consisting of 60 trials each; during the first two blocks TMS was delivered to one hemisphere and during the last two blocks TMS was delivered to the other hemisphere (i.e. a prime block and a repeat block of sounds associated with the stimulation of each hemisphere). The order of stimulated hemisphere was counterbalanced across subjects. During TMS to the hand representation within the right hemisphere MEPs from the left FDI were recorded and vice versa. Recording electrodes were mounted on the belly of the FDI (after cleaning with abrasive gel and alcohol); ground and reference electrodes (unipolar montage) were placed on the left upper arm for the recordings of the left hand signal and on the right upper arm for the recordings of the right hand signal (as in Aziz-Zadeh et al. 2004). Digitization sampling rate was 1,000 Hz. Single transcranial magnetic pulses (Magstim Rapid2 Transcranial Magnetic Stimulator, Magstim Company, Spring Gardens, UK) were delivered by an eight-figure coil to the hand representation within the primary motor cortex 2.0; 2.25; 2.5; 2.75; or 3.0 s post-stimulus onset (random attribution of the interval). The hand area was identified for each subject as the optimal site to elicit motor hand response (as in Aziz-Zadeh et al. 2004). The motor threshold was determined as the minimal intensity which induced MEPs >50 µV peak-to-peak amplitude in at least five out of 10 trials (as in Aziz-Zadeh et al. 2004). For MEP recordings, single-pulse TMS was delivered at 120 % of the motor threshold of the subject and hemisphere.

MEP data were band-pass filtered between 0.3 and 500 Hz (with 50 Hz notch filter), baseline corrected over the 100 ms pre-stimulus period, and checked for TMS-unrelated modulations of similar or larger amplitudes than those of the MEPs. For each subject and hand, valid MEPs were averaged over the period 100 ms prior to the TMS pulse to 200 ms after it for five conditions: (i) all trials; (ii) initial presentations of M+ sounds; (iii) repeated presentations of M+ sounds; (iv) initial presentations of M− sounds; and (v) repeated presentations of M− sounds (Fig. 1). Values for (ii)–(v) were normalized for each subject and hand as percentage of (i). Normalized MEPs from the right and left hand were analyzed separately using a 2 × 2 within subject repeated measures ANOVA with the factors category (M+ vs. M−) and presentation (initial vs. repeated).

Results

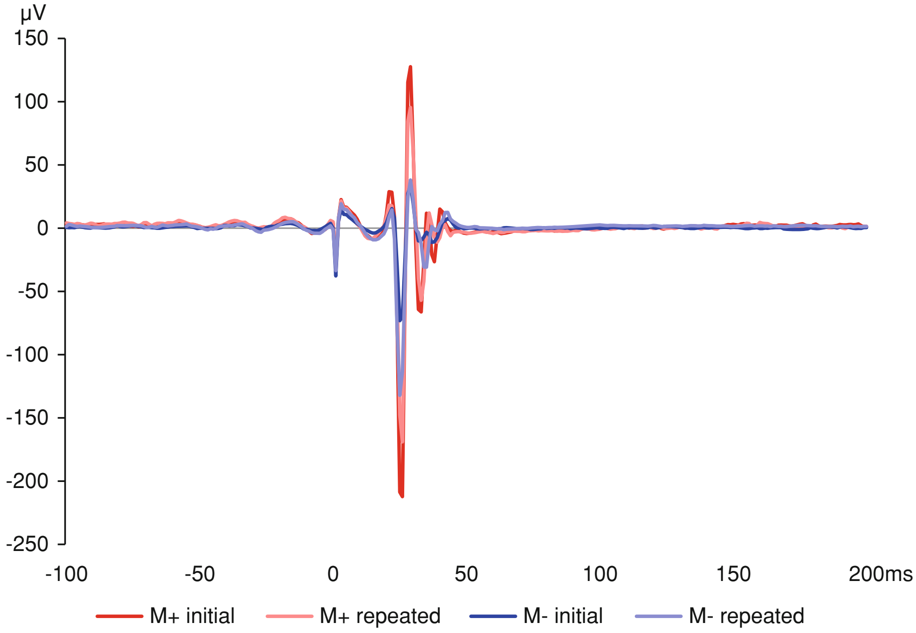
A repeated measure ANOVA applied to MEPs from left FDI revealed a significant interaction of factors category and presentation ($F_{(1,14)} = 8.12$; $p < 0.05$), a significant main effect of category ($F_{(1,14)} = 5.12$; $p < 0.05$) but not of presentation ($F_{(1,14)} = 3.72$; $p = 0.07$). Post hoc *t* tests revealed a significantly smaller MEPs for repeated than initial presentations of M+ ($t_{(1,14)} = 2.66$; $p < 0.05$; Fig. 2) but not M− sounds ($t_{(1,14)} = 0.95$; $p = 0.36$). Furthermore, MEPs were significantly larger for initial presentations of M+ than of M− sounds ($t_{(1,14)} = 2.88$; $p < 0.05$); no such difference was present for repeated presentations of M+ and M− sounds ($t_{(1,14)} = 0.66$; $p = 0.52$).

A repeated measure ANOVA applied to MEPs from right FDI revealed that the main effect of category failed to reach the significance level ($F_{(1,15)} = 3.98$; $p = 0.06$), presentation ($F_{(1,15)} = 1.20$; $p = 0.29$) or interaction ($F_{(1,15)} = 0.02$; $p = 0.90$).

Discussion

This is a first report of repetition suppression in MEPs while subjects listen to initial and repeated presentations of the same manual-action-related sound. Our results demonstrate that auditory afferents to motor neurons carry

Fig. 1 Average MEPs from left FDI elicited by TMS to right hand area in a typical subject



semantic information which distinguishes individual items within the category of action-related sounds; this is a much finer discrimination than the previously reported difference between categories (manual-action-related versus manual-action-unrelated sounds; Aziz-Zadeh et al. 2004). The auditory motor link can be accounted for in three different ways, two of which imply high level semantic information. First, the auditory-motor link could represent a remnant of a phylogenic ready-for action system and be dedicated to low-level motor representations. Repetition priming of motoneuronal activity has been previously described in the feeding network of aplysia, where repeated stimulation led to an increase in the firing rate of neurons (Friedman et al. 2009). The repetition enhancement has been interpreted as an intrinsic characteristic of a network dedicated to motor behavior (Friedman and Weiss 2010). Such an interpretation is, however, unlikely for our results. We observed repetition suppression of the motor output, which suggests that the auditory-motor is likely to be involved in higher-order representations. Second, the auditory-motor link could be part of the mirror neuron system and be thus dedicated to a combined perceptual and motor representation. The mirror neurons have been described in animal models as responding both during the execution of an action and to the (visual or auditory) perception of it (Rizzolatti et al. 1996; see Kohler et al. 2002 and Keysers et al. 2003 for auditory stimuli). In man the mirror system was proposed to comprise a fronto–temporo–parietal network, which was shown to be activated by both action perception and execution (Rizzolatti et al. 2001; Pulvermuller and Fadiga 2010; Mukamel et al. 2010). More specifically, both listening to actions and executing them was shown to activate left BA44 and BA6 as well as parietal and temporal regions (Gazzola et al. 2006). Repetition suppression has been reported within the mirror system in the left prefrontal cortex using visually presented words as primes and action-related sounds as targets (Galati et al. 2008). The item-specific repetition priming effect, which we have demonstrated at the level of the motor output, could be thus interpreted as part of the mirror system. Third, the auditory motor link could have an essentially perceptual role as part of the semantic representation of action-related sounds. Repetition suppression has been repeatedly shown to be a robust characteristic of semantic representations of environmental sounds, in particular on the left temporal convexity (Bergerbest et al. 2004; Murray et al. 2008; De Lucia et al. 2010; Bourquin et al. 2012). Its occurrence at the level of the auditory-motor link is a strong argument for considering the motor cortex as part of auditory semantic representations. Such an interpretation calls, however, for a reconsideration of modular models, which consider that stimuli are extensively processed within sensory cortices and that the feedforward projections to motor cortex do not play a role in perception (Pulvermuller and Fadiga 2010).

Current evidence suggests that motor representation of action-related sounds involves both hemispheres. The parieto–frontal representations of action-related sounds were reported within the left (Lewis et al. 2005; Pizzamiglio et al. 2005; Gazzola et al. 2006; Hauk et al. 2006; Doehrmann et al. 2008) or, in a few studies, in the right (Lepage et al. 2010) or both hemispheres (Lahav et al. 2007; De Lucia et al. 2009). In our study main effect of category was significant upon right hemispheric stimulation ($p < 0.05$; no such effect was

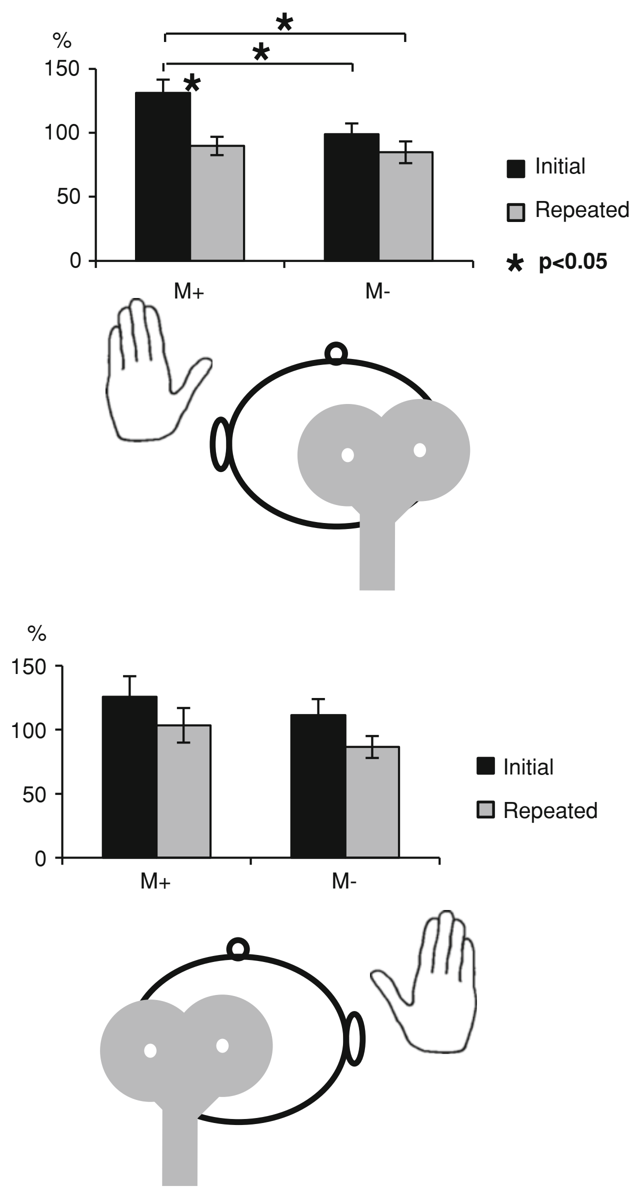


Fig. 2 MEP modulations by sound category (M+, M−) and repetition in left (*top*) and right FDI (*bottom*). MEPs are indicated as percentage of mean MEP per subject and hemisphere

found upon left hemispheric stimulation: $p = 0.06$). A previous study reported a significant increase of MEPs upon left hemispheric TMS stimulation, no such effect was observed upon right hemispheric TMS (Aziz-Zadeh et al. 2004); we would like to argue that the negative results for right hemispheric TMS in this study are due to a repetition effect, since only two hand-related sounds were used, typing and tearing paper, each presented 20 times. As demonstrated here, the right hand area is sensitive to repeats and may be even more so to numerous repetitions as is the predominantly right hemispheric auditory temporo–parietal network (Bourquin et al. 2012).

The putative hemispheric difference in the motor representation of action-related sounds needs to be investigated further. As suggested by a recent study, the two hemispheres may code for different aspects of the auditory-motor relationship; having learned to play a musical piece was shown to increase activation of Broca's area and premotor cortex during passive listening to the same tones ("hearing–doing"; Lahav et al. 2007). Present only for the learned melody within the left hemisphere, the effect was generalized for other melodies in the right hemisphere, suggesting a motor versus perceptual lateralization.

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References

Aziz-Zadeh L, Iacoboni M, Zaidel E, Wilson S, Mazziotta J (2004) Left hemisphere motor facilitation in response to manual action sounds. Eur J Neurosci 19(9):2609–2612. doi:10.1111/j.0953-816X.2004.03348

Bergerbest D, Ghahremani DG, Gabrieli JD (2004) Neural correlates of auditory repetition priming: reduced fMRI activation in the auditory cortex. J Cogn Neurosci 16(6):966–977. doi:10.1162/0898929041502760

Bourquin NM, Spierer L, Murray MM, Clarke S (2012) Neural plasticity associated with recently versus often heard objects. NeuroImage 62(3):1800–1806. doi:10.1016/j.neuroimage.2012.04.055

De Lucia M, Camen C, Clarke S, Murray MM (2009) The role of actions in auditory object discrimination. NeuroImage 48(2):475–485. doi:10.1016/j.neuroimage.2009.06.041

De Lucia M, Cocchi L, Martuzzi R, Meuli RA, Clarke S, Murray MM (2010) Perceptual and semantic contributions to repetition priming of environmental sounds. Cereb Cortex 20(7):1676–1684. doi:10.1093/cercor/bhp230

Doehrmann O, Naumer MJ, Volz S, Kaiser J, Altmann CF (2008) Probing category selectivity for environmental sounds in the human auditory brain. Neuropsychologia 46(11):2776–2786. doi:10.1016/j.neuropsychologia.2008.05.011

Friedman AK, Weiss KR (2010) Repetition priming of motoneuronal activity in a small motor network: intercellular and intracellular signaling. J Neurosci 30(26):8906–8919

Friedman AK, Zhurov Y, Ludwar B, Weiss KR (2009) Motor outputs in a multitasking network: relative contributions of inputs and experience-dependent network states. J Neurophysiol 102(6):3711–3727. doi:10.1152/jn.00844.2009

Galati G, Committeri G, Spitoni G, Aprile T, Di Russo F, Pitzalis S, Pizzamiglio L (2008) A selective representation of the meaning of actions in the auditory mirror system. NeuroImage 40(3):1274–1286. doi:10.1016/j.neuroimage.2007.12.044

Gazzola V, Aziz-Zadeh L, Keysers C (2006) Empathy and the somatotopic auditory mirror system in humans. Curr Biol : CB 16(18):1824–1829. doi:10.1016/j.cub.2006.07.072

Grill-Spector K, Henson R, Martin A (2006) Repetition and the brain: neural models of stimulus-specific effects. Trends Cogn Sci 10(1):14–23. doi:10.1016/j.tics.2005.11.006

Hauk O, Shtyrov Y, Pulvermuller F (2006) The sound of actions as reflected by mismatch negativity: rapid activation of cortical sensory-motor networks by sounds associated with finger and tongue movements. Eur J Neurosci 23(3):811–821. doi:10.1111/j.1460-9568.2006.04586.x

Henson RN (2003) Neuroimaging studies of priming. Prog Neurobiol 70(1):53–81

Keysers C, Kohler E, Umilta MA, Nanetti L, Fogassi L, Gallese V (2003) Audiovisual mirror neurons and action recognition. Exp Brain Res Exp Hirnforschung Exp cereb 153(4):628–636. doi:10.1007/s00221-003-1603-5

Kohler E, Keysers C, Umilta MA, Fogassi L, Gallese V, Rizzolatti G (2002) Hearing sounds, understanding actions: action representation in mirror neurons. Science 297(5582):846–848. doi:10.1126/science.1070311

Lahav A, Saltzman E, Schlaug G (2007) Action representation of sound: audiomotor recognition network while listening to newly acquired actions. J Neurosci 27(2):308–314. doi:10.1523/JNEUROSCI.4822-06.2007

Lepage JF, Tremblay S, Nguyen DK, Champoux F, Lassonde M, Theoret H (2010) Action related sounds induce early and late modulations of motor cortex activity. NeuroReport 21(4):250–253

Lewis JW, Brefczynski JA, Phinney RE, Janik JJ, DeYoe EA (2005) Distinct cortical pathways for processing tool versus animal sounds. J Neurosci 25(21):5148–5158. doi:10.1523/JNEUROSCI.0419-05.2005

Mukamel R, Ekstrom AD, Kaplan J, Iacoboni M, Fried I (2010) Single-neuron responses in humans during execution and observation of actions. Curr Biol : CB 20(8):750–756. doi:10.1016/j.cub.2010.02.045

Murray MM, Camen C, Spierer L, Clarke S (2008) Plasticity in representations of environmental sounds revealed by electrical neuroimaging. NeuroImage 39(2):847–856. doi:10.1016/j.neuroimage.2007.09.002

Oldfield RC (1971) The assessment and analysis of handedness: the Edinburgh inventory. Neuropsychologia 9:97–113

Pizzamiglio L, Aprile T, Spitoni G, Pitzalis S, Bates E, D'Amico S, Di Russo F (2005) Separate neural systems for processing action- or non-action-related sounds. NeuroImage 24(3):852–861. doi:10.1016/j.neuroimage.2004.09.025

Pulvermuller F, Fadiga L (2010) Active perception: sensorimotor circuits as a cortical basis for language. Nat Rev Neurosci 11(5):351–360. doi:10.1038/nrn2811

Rizzolatti G, Fadiga L, Gallese V, Fogassi L (1996) Premotor cortex and the recognition of motor actions. Brain Res Cogn Brain Res 3(2):131–141

Rizzolatti G, Fogassi L, Gallese V (2001) Neurophysiological mechanisms underlying the understanding and imitation of action. Nat Rev Neurosci 2(9):661–670. doi:10.1038/35090060