Sound and Movement

Komeilipoor, N.

2015

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Summary

In this thesis, I investigated how we detect and select sounds, distill information, and use them to perform appropriate actions in the environment. I put particular focus on the interaction between sound perception and motor behavior, put that into context of embodied cognition, and sought to unravel its neural underpinnings. I either modified the cognitive context and tested to what extend this modification altered the motor system, or – in the final study of the thesis – I modified the motor system and tested how this altered cognitive capacities.

After a general, yet brief overview of the challenges in the fields of sound perception and motor control in the introductory *Chapter 1,* I circled around the following questions in the subsequently summarized studies:

i. Does valence of sound affect the excitability of the corticospinal motor tract?
ii. Does speech perception through the observation of gestures alter M1 excitability?
iii. What strategies can be used to intercept moving sounds?
iv. Do non-temporal aspects of musical sound affect movement timing?
v. What are the cortical correlates of audiomotor and audiovisual integration?

In *Chapter 2,* I investigated how emotional processing of non-verbal auditory stimuli leads to increased corticospinal tract excitability, to what degree this modulation is lateralized in response to the valence of the stimuli, and whether delivering sounds to the left ear, right ear, or both ears may yield lateralization in motor facilitation. During the experiment, subjects listened to sounds (monaurally and binaurally), and single-pulse TMS was delivered to either left or right primary motor cortex. The EMG activities recorded from the contralateral abductor pollicis brevis muscle revealed significant changes in motor-evoked potentials, which is interpreted as an increase in corticospinal tract (CST) excitability in response to unpleasant as compared to neutral sounds. That increase was lateralized as a function of stimulus valence: Unpleasant stimuli resulted in a significantly larger CST excitability in the left hemisphere, while pleasant stimuli yielded a greater CST excitability in the right one. Furthermore, the motor evoked potentials were larger when listening to unpleasant sounds with the left than with the right ear. In the chapter, I argued in detail that the facilitation of CST excitability in the left

primary motor cortex in response to unpleasant sounds suggests a general preference for a direct motor-auditory projection for processing threatening auditory stimuli. This system may have been developed to allow for rapid fight-or-flight responses to potential dangerous stimuli.

In *Chapter 3,* I continued with altering the cognitive context to test for corresponding effects in the motor system. I addressed the question whether or not observation of newly learned hand gestures paired and not paired with words may result in changes in the excitability of the hand and tongue areas of motor cortex. Once again, I used single-pulse TMS and measured motor excitability, this time in tongue and hand areas of left primary motor cortex. Subjects viewed video sequences of bimanual hand movements associated or not associated with nouns. I found higher motor excitability in the tongue area during the presentation of meaningful gestures (noun-associated) as opposed to meaningless ones, while CST excitability of hand motor area was not differentially affected by gesture observation. These results let me conclude that the observation of gestures associated with a word results in activation of articulatory motor network accompanying speech production.

In contrast to the previous two, in the experiment outlined in *Chapter 4,* subjects had to move themselves, which offered the possibility to investigate more dynamical issue rather than the analysis of static percepts. I examined the ability to intercept a laterally moving virtual sound object by controlling the displacement of a sliding handle. I tested whether the interaural time difference (ITD) of an arriving sound might be the main source of perceptual information for successfully intercepting the object. The experimental findings revealed that in order to accomplish the task, one might need to vary the duration of the movement, control the hand velocity and time to reach the peak velocity (speed coupling), while the adjustment of movement initiation does not facilitate performance. The overall performance was more successful when the subjects employed a time-to-contact (tau) coupling strategy. Sound seems to contain prospective information to guide goal-directed actions.

Coming back to the topic of the valence of sound, in *Chapter 5*, I sought to tackle the influence of its 'color'. The origins of consonance and dissonance in terms of acoustics, psychoacoustics and physiology have been debated for centuries, indeed, but their plausible effects on movement synchronization had largely been ignored. I asked whether timing, as in the previous chapter, plays a role in processing consonant versus dissonant sounds. In this chapter, I summarized the effects of musical consonance/dissonance on sensorimotor timing in a synchronization-continuation paradigm during which participants performed reciprocal aiming movements. I compared movements synchronized to either consonant or to dissonant sounds and showed that they were differentially influenced by the degree of consonance of the sound presented. The difference was present after the sound stimulus had been removed. The performance measured after consonant sound exposure was more stable and accurate, with a strong information/movement coupling (tau-coupling) and pronounced movement circularity. It appears that the neural resonance representing consonant tones yields finer perception/action coupling, which, in turn, may explain the prevailing preference for these types of tones.

From the first chapters it should be clear the perception of sound is affected by various factors. In the particular case of speech sound, just looking at facial motions can have a major influence. Incongruity between sounds and watching somebody articulating them may cause a bias toward the visual percept. This phenomenon is referred to as the McGurk effect. In *Chapter 6,* I addressed brain mechanisms underlying (the failure of) audiovisual as well as audiomotor multisensory integration in the McGurk effect. In the experiment, listeners had to recognize auditory syllables while silently articulating congruent/incongruent syllables (motor condition) or observing videos of a speaker's face articulating the syllables (visual condition), and EEG responses were recorded during all the conditions. When incongruent syllables were observed and when silently articulated, perception of sound was diminished. This was accompanied by significant amplitude modulations in the beta frequency band in right superior temporal areas. There, the event-related beta activities during congruent conditions were phase locked to responses evoked during the auditory only condition. This implies that proper temporal alignment of different input streams in right superior temporal areas is mandatory for both audiovisual and audiomotor speech integration.

In the finalizing epilogue, *Chapter 7*, I recalled the aforementioned research questions point by point:

i. Valence of sound does affect the excitability of the corticospinal motor tract: Unpleasant stimuli increase the CST excitability in left M1 and pleasant ones in right M1.
ii. Speech perception through observation of gestures alters M1 excitability in the tongue area if gestures are associated with words.
iii. To intercept moving virtual sounds, individuals employed a time-to-contact (tau) coupling strategy and adjusted kinematic parameters such as movement duration, peak velocity and time to reach the peak velocity.
iv. Movement timing measured after exposure to a consonant metronome is more precise and less variable than the timing following a dissonant metronome.
v. Differences of proper versus improper audiomotor or audiovisual integration are primarily visible in the superior temporal area where it correlates with the degree of beta-frequency phase synchronization.

Despite all efforts summarized in the thesis, the interaction between sound perceptions and motor actions at behavioral and neural levels is still not fully understood. Future research is required especially to comprehend more complex, audiomotor skills such as those found among musicians and visually impaired people.

Samenvatting

Centraal in dit proefschrift stond de vraag hoe we geluiden detecteren en selecteren en zo informatie verzamelen teneinde adequate acties uit te voeren. Om deze vraag te beantwoorden is een vijftal experimenten uitgevoerd. In alle experimenten werd de interactie tussen de perceptie van geluid en 'eenvoudig' motorische acties onderzocht op zowel gedrags- als neurofysiologisch niveau.

Na een kort, inleidende overzicht over actuele thema's op het gebeid van geluidswaarneming en motorische controle (*Hoofdstuk 1*), kwamen de volgende onderzoeksvragen aan bod:

i. Heeft de valentie ('valence' oftewel het belang) van geluid invloed op de prikkelbaarheid van corticospinale banen?
ii. Verandert de prikkelbaarheid van de primaire motorcortex door waarneming van gebaren die een woord representeren (zoals in gebarentaal)?
iii. Welke strategieën worden gebruikt voor het onderscheppen van bewegende virtuele objecten op geleide van geluid?
iv. Beinvloeden niet-temporele aspecten van geluid de temporele controle van bewegingen?
v. Wat zijn de corticale correlaten van audiomotorische en audiovisuele integratie?

In de studie gerapporteerd in *Hoofdstuk 2* werd onderzocht hoe het emotioneel verwerken van niet-verbale, akoestische stimuli de exciteerbaarheid van de corticospinale banen verhoogt en in hoeverre deze modulatie gelateraliseerd is als functie van de valentie van die stimuli. Daarnaast werd onderzocht of het luisteren met alleen het linker- of het rechteroor dan wel met beiden oren een lateralisatie van de exciteerbaarheid van de corticospinale banen veroorzaakt. In het experiment luisterden proefpersonen naar verschillende geluiden terwijl de linker of rechter primaire motorcortex met behulp van ('single pulse') TMS werd geprikkeld. In de contralaterate m. abductor pollicis brevis werd hierdoor een EMG potentiaal geëvoceerd die als marker voor de exciteerbaarheid van de betreffende corticospinale banen beschouwd wordt. De EMG-potentiaal was significant groter indien de proefpersonen voorafgaand aan de TMP-puls naar een onaangenaam geluid luisterden dan wanneer ze naar een aangenaam of een neutraal ge-

luid luisterden. Dit effect was gelateraliseerd: een onaangenaam geluid veroorzaakte een grotere exciteerbaarheid in de linker hemisfeer, terwijl een aangenaam geluid de exciteerbaarheid in de rechter hemisfeer verhoogde. Tevens waren de EMG-potentialen groter als met het linker oor dan als met het rechteroor naar onaangename geluiden werd geluisterd. Deze resultaten suggereren het bestaan van directe projecties van de auditieve op de motorische hersenschors ten behoeve van een snelle verwerking van onaangename dan wel bedreigende geluiden (‘fight-or-flight’ respons).

In *Hoofdstuk 3* is een studie beschreven over waarneming van recent geleerde handgebaren. Daarin werd onderzocht of de deze invloed heeft op de exciteerbaarheid van de hand- of tongrepresentatie in de primaire motorcortex, en dit als functie van de betekenis van het gebaar (wel of geen betekenis). Evenals in het in hoofdstuk 2 beschreven onderzoek werd de hersenschors met behulp van (‘single-pulse’) TMS geprikkeld. Deze prikkeling werd nu echter beperkt tot de linker-hemisfeer, waarin bij rechtshandige personen de gebieden van Broca en Wernicke gelokaliseerd zijn. Vervolgens werd het EMG van handspieren en van de tong gemeten. Tijdens het experiment keken de proefpersonen naar video-opnamen van handgebaren die wel (betekenisvol) of niet (betekenisloos) met zelfstandige naamwoorden geassocieerd waren. De exciteerbaarheid van het tonggebied was significant hoger indien de gebaren betekenisvol waren dan wanneer ze betekenisloos waren, terwijl de exciteerbaarheid van het handgebied daardoor niet werd beïnvloed. Dit wijst erop dat de visuele waarneming van betekenisvolle gebaren het articulatorisch-motorische netwerk activeert, een netwerk dat normaliter bij de productie van taal betrokken is.

In het in *Hoofdstuk 4* beschreven experiment stond de interceptie van lateraal bewegende virtuele objecten op basis van geluid centraal. Onderzocht werd of zo’n interceptie, via een hendelbeweging, mogelijk was op grond van de informatie die geleverd wordt door het tijdsverschil tussen de aankomst van het geluid bij beide oren. Dit bleek het geval te zijn, waarbij variaties in bewegingsduur, -snelheid, en -versnelling, maar niet de variaties in startmoment van de beweging, garant stonden voor het succes van de interceptie. Kennelijk maakten de proefpersonen gebruik van een ‘time-to-contact’ koppelingsstrategie tussen het geluid en de beweging.

Ondanks het feit dat consonanten en dissonanten in de (psycho-)akoestiek en in de fysiologie al zeer lang onderzocht worden, is nauwelijks bekend of ritmische bewegingen beter op consonanten dan op dissonanten afgestemd kunnen worden. In *Hoofdstuk 5* wordt een experiment beschreven waarin dit is onderzocht. Proefpersonen werd gevraagd om ritmische vingerbewegingen te synchroniseren met via een metronoom gepresenteerde toontjes en deze bewegingen vervolgens door te zetten na beëindiging van de toonpresentaties, een opzet die in de literatuur als synchronisatie-continuering paradigma bekend staat. Tijdens de continueringsfase bleek er van een minder variabele, betere uitvoering sprake te zijn na synchronisatie met consonante dan met dissonante toontjes. Kennelijk werd het oorspronkelijk ritme in de sequenties van consonante toontjes beter opgepikt dan in sequenties van dissonante toontjes, wat de voorkeur voor consonante boven dissonante tonen zou kunnen verklaren.

Waar in het bovenbeschreven onderzoek sprake was van relatief simpele geluiden, werden in het onderzoek dat in *Hoofdstuk* 6 aan de orde komt talige akoestische stimuli gepresenteerd. Het is reeds lang bekend dat de waarneming daarvan verandert indien tegelijkertijd naar een gezicht gekeken wordt waarvan de mondbewegingen incongruent zijn met de gearticuleerde stimulus. Er ontstaat dan een 'bias' ten faveure van de visuele waarneming, het zogenoemde McGurk effect, dat het onderwerp vormt van hoofdstuk 6. In dit hoofdstuk ging ik op zoek naar mogelijke neurale mechanismen die ten grondslag liggen aan (het falen van) audiovisuele of audiomotorische integratie bij het McGurk effect. Proefpersonen luisterden naar syllaben en moesten deze identificeren hetzij zonder dat een andere taak uitgevoerd moest worden (controle conditie), hetzij in een situatie waarin ze tijdens de identificatietaak geluidloos congruente of incongruente syllaben moesten articuleren (motorische condities), dan wel in een situatie waarin ze videobeelden bekeken van een spreker die congruente of incongruente syllaben uitsprak (visuele condities). In het experiment werd de corticale activiteit met behulp van EEG gemeten. Het bleek dat de identificatietaak in zowel de incongruente motorische conditie als in de incongruente visuele conditie slechter verliep dan in de controleconditie. Deze achteruitgang ging gepaard met een significante amplitudemodulatie in de bèta-frequentieband van het superior temporale gebied van de rechter hersenhelft. Dit gebied speelt een belangrijke rol bij de integratie van multi-sensorische input. De bèta-activiteit aldaar bleek in de congruente condities fase-gekoppeld te zijn aan de bèta-activiteit in de controle-conditie tijdens welke alleen de te identificeren syllaben werden gepresenteerd. In de incongruente condities was dat niet het geval. Het lijkt erop dat in dit geval de concurrerende input in het superior temporale gebied (veroorzaakt door articulatie of door visuele input) de fase van de beta-activiteit verstoorde en kennelijk is deze fase, oftewel de timing van het beta-ritme, van belang om verschillende sensorische inputs goed te integreren.

In de epiloog (*Hoofstuk 7*) komen de vijf onderzoeksvragen opnieuw aan bod en worden de volgende conclusies geformuleerd:

i. De valentie van geluid heeft invloed op de prikkelbaarheid van de corticospinale banen: onaangename en aangename akoestische stimuli verhogen de prikkelbaarheid in respectievelijk de linker en rechter primaire motorcortex.
ii. Visuele waarneming van gebaren verandert de prikkelbaarheid in het corticale tonggebied indien ze betekenisvol zijn (geassocieerd met woorden).
iii. Het onderscheppen van bewegende, virtuele objecten op basis van geluid vindt plaats via een 'time-to-contact' koppelings-strategie waardoor kinematische parameters zoals bewegingsduur en pieksnelheid kunnen worden aangepast.
iv. Het synchroniseren van ritmische bewegingen met consonante toontjes van een metronoom verloopt beter (nauwkeuriger en minder variabel ritme) dan synchronisatie met dissonante toontjes.
v. Beta-activiteit in het superior temporale gebied van de rechter hersenhelft speelt een belangrijke rol als corticaal correlaat van audiomotorische en audiovisuele integratie.

Het moge duidelijk zijn dat ook na de in dit proefschrift gerapporteerde resultaten het inzicht in de interacties tussen akoestische waarneming en motorische acties nog verre van volledig is, en dat dit zowel geldt op gedragsniveau als op neuraal niveau. Verder onderzoek is nodig, in het bijzonder ter opheldering van de complexe audiomotorische vaardigheden, zoals die bijvoorbeeld ten toon worden gespreid door musici en door slechtzienden en blinden.

Acknowledgments

My gratitude is extended to the following people who have helped me, in one way or another, to complete the works described in this thesis. First and foremost, I would like to gratefully and sincerely express my deepest appreciation to my two supervisors, Andreas Daffertshofer in Amsterdam and Paola Cesari in Verona. Their patience, encouragement, guidance, understanding, immense knowledge, and most importantly, friendship were key motivation throughout my PhD. Andreas, thank you for being my mentor, editor, proofreader and sounding board. Paola, thank you so much for all your support and for helping me find my own path whilst showing me which paths I might be missing. Many thanks also have to go to Cathy Craig who supervised me during my stay in Belfast and provided me with all her invaluable advice. I would also like to express my gratitude to all my collaborators and the co-authors: Carmelo Vicario, Matthew Rodger, Fabio Pizzolato and Ivan Camponogara for their help, support and guidance. I would like to thank Dr. John Stins for offering thorough and excellent feedback on an earlier version of this thesis. Thanks Dragoș Lazarin for helping me in designing the cover of my thesis.

Special thanks must go to all my friends around the world who have touched me with love and kindness. Thank you for your friendship, support, hugs, laughs, cups of coffee and glasses of wine along the way. Thank you for granting me a sense of belonging.

Finally, I would like to thank my parents, Aliyeh and Fereydoon, from the bottom of my heart. You have inspired me to follow my dreams and done everything you could to put me on the path toward success. I am forever deeply indebted to you for all you have sacrificed for me. Also, a huge thank you to my father, Fereydoon, for going above and beyond his duty as a proofreader to read and edit every line of the manuscript and paying scrupulous attention to details. Thanks also to my lovely brothers: Nima and Nariman who have been so supportive in whatever I do in my life.