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## Sound and Movement

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## *Chapter 7*

### **Epilogue**

We use information embedded in sounds to perform appropriate actions in the environment. In my thesis, I summarized different attempts to tackle the interaction between our auditory and motor systems from different perspectives. In this final chapter, I will first provide point-by-point answers to the questions listed in the general introduction (*Chapter 1*). Thereafter, I will continue with the story to end our stroll through Amsterdam.

#### **Answers to research questions**

Does valence of sound affect the excitability of the corticospinal motor tract?

In *Chapter 2*, I addressed this question and found a significant increase in the corticospinal motor tract (CST) excitability in response to unpleasant sounds. The increased excitability was lateralized as a function of stimulus valence: Unpleasant stimuli resulted in significantly higher facilitation of motor potentials evoked in the left hemisphere, while pleasant stimuli yielded a greater CST excitability in the right one. Furthermore, TMS induced higher motor evoked potentials when listening to unpleasant sounds with the left than with the right ear.

Does speech perception through observation of gestures alter M1 excitability?

*Chapter 3* was devoted to this question by discussing whether observation of newly learned hand gestures paired and not paired with words result in changes in the excitability of the hand and tongue areas of motor cortex. Using TMS, we measured motor excitability in tongue and hand areas of left M1, while participants were watching video sequences of bimanual hand movements associated or not associated with nouns. The highest cortical excitability occurred in the tongue area during the presentation of word-associated gestures compared to gestures not associated with any words (meaningless). On the contrary, hand motor areas presented the same level of excitability for both types of gestures.

What strategies can be used to intercept moving sounds?

In the study reported in *Chapter 4*, I showed how a simple variable such as the interaural time difference (ITD) of an arriving sound could provide sufficient information for participants to intercept a laterally moving sound object. Overall, our results 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. Furthermore, overall performance was more successful when subjects employed a time-to-contact ( $\tau$ ) coupling strategy.

Do non-temporal aspects of musical sounds affect movement timing?

In *Chapter 5*, I tested the effects of musical consonance/dissonance on sensorimotor timing in a synchronization-continuation paradigm during which participants performed reciprocal aiming movements. Remarkably, the movement performance measured after exposure to a consonant, as compared to a dissonant metronome, was found to be less variable and more precise, with a higher percentage of information/movement coupling ( $\tau$ -coupling) and a higher degree of movement circularity (indicating a smoother oscillatory motion).

What are the cortical correlates of audiomotor and audiovisual integration?

Finally, in *Chapter 6*, EEG served to identify cortical responses during the perception of auditory syllables influenced by observation and silent articulation of congruent/incongruent syllables. The perception of sounds diminished when incongruent syllable were observed and also when subjects silently articulated the syllables, albeit to a lesser degree. This was accompanied by an amplitude modulation in beta frequency bands in the right superior temporal areas. There, the event-related activities during the congruent condition were phase locked to the responses evoked during the auditory only condition. This indicates that phase locking in the beta band in auditory cortex is paramount for audiovisual and audiomotor speech integration.

## **How do sound and movement relate?**

For at least six reasons, there is a close relationship between sound and movement.

Sound is a direct consequence and an indicator of motion; as shown in the example in the *Introduction*, when you ring your bicycle's bell, the sound made is a consequence of your action.

Passively listening to sounds activates the motor system, e.g., non-verbal emotional sounds (*Chapter 2*), music and speech sounds.

The production of sounds such as music requires and inevitably causes movement, as seen in our example in the *Introduction* when you start spontaneously to tap your foot in time with a rhythm's beat.

Information embedded in a sound can help us to purposefully control goal-directed behaviors; as shown in *Chapter 4*, the interaural time difference (ITD) can provide sufficient information to intercept a moving sound object.

Spatiotemporal properties of action can be affected by non-temporal properties of sound; as shown in *Chapter 5*, the degree of consonance of the musical sound presented influenced the types of movement produced after the sound stimulus was removed.

Movement can influence the perception of the sound; in *Chapter 6*, I showed that the perception of auditory syllables can be disturbed or improved when the listener silently articulates incongruent or congruent syllables, respectively.

## **Hearing the future**

*Let's go back to the Dam Square where the band is playing its final song "Dark was the night, cold was the ground". That gorgeous song has been written by "Blind Willie Johnson"... The last notes fade out, and it is the time to put a few coins into the guitarist's baseball cap and head back home. You might want to ask him whether he really plays the 'beep baseball'. If the answer is "yes", then you may wonder what sort of auditory information lets him anticipate the ball's arrival?*

There are numerous acoustic 'dimensions' that are considered informative about the approach of a sound source: the differences in both the intensity and arrival time of sound when reaching the left versus the right ears, or the frequency changes induced by the Doppler shift may enable listeners to reliably indicate when and where a moving

sound source is passing (Rosenblum et al., 1987). Take the interaural intensity and time differences (ITD) as an example. As a baseball approaches from one side of the player, its sound reaches one ear before the other and it is perceived to be louder. This provides anticipatory information and allows the players to anticipate the arrival of the ball. The changing sounds inform the player about upcoming events, i.e. sounds allow the players to *hear the future*. But what are the movement strategies that the players use to guide their actions when relying solely on auditory information? In *Chapter 4*, I showed how the ITD of an arriving sound may provide sufficient information for participants to intercept a laterally moving sound object. I showed that it is the duration and velocity of the movement and not the time of its initiation that causes a difference in successful and failed performances. This highlights the need to adjust movement duration and velocity to the information specifying the moving auditory object's time to arrival in order to successfully intercept it. To put it differently, participants used ITD as a reliable source of information that not only specifies the direction in which the sound source is travelling, but serves as online control for interception action. While subjects may have used a 'variable movement initiation time/constant movement duration' strategy to intercept the moving sound, the overall performance was more successful when they employed a tau coupling strategy. Hence, sound contains prospective information to guide goal-directed actions.

### **Music changes the way you move**

*Off Dam Square, you still imagine the beat. You tapped your foot and still want to go with the beat. Would that be different if the music were a low pitch blues?*

Is movement to a rhythm influenced by non-temporal characteristics of music like the pitch? If you were asked to continue tapping your foot with the same tempo when the music stopped playing, do you think the pattern of movement you produced would be affected by what you had listened to before?

We move to make music but music also makes us move. Perception of temporal regularity (beat) in music is believed to guide this synchronization. In *Chapter 5*, I investigated whether non-temporal aspects of musical sounds do indeed affect movement timing. Different pitch relationships between tones lead to differences in perceived conso-

nance (pleasantness) of sounds in humans. This perceptual difference is present even in four-month-old babies (Zentner and Kagan, 1998). It is also found to be both cross-cultural (Fritz et al., 2009) and to have similar physical principles that rule human vocalization (Schwartz et al., 2003). Not surprisingly, the consonant intervals occur more often than the dissonant ones in tonal music (Vos and Troost, 1989). While ancient as well as contemporary scholars have been trying to define differences in the perception of consonance and dissonance at mathematical or physical levels, recent neuroimaging studies have shown these differences at both cortical (e.g., PM1: Minati et al., 2009) and subcortical levels (e.g., brainstem: Bidelman and Krishnan, 2009, 2011). Given the ecological relevance of consonance versus dissonance, the question is whether the harmonic structure of sounds affects the spatiotemporal characteristics of movements when it is used as a guide for timed actions. I addressed the effects of consonance/dissonance musical intervals on movement synchronization in a synchronization-continuation paradigm. The movement performance measured during the synchronization was not influenced by the degree of musical consonance, while the reciprocal movements made after exposure to a consonant, as opposed to a dissonant, was found to be different both in terms of timing and form. One may infer that the neural resonance representing consonant tones leads to finer perception/action coupling, which in turn may help explain the prevailing preference for these types of tones.

### **Listening to the good, the bad and the neutral**

*It is late when you leave the city. You again hear some pleasing sounds that catch your attention and make you stop and listen. Not even a block further you hear sounds that you didn't like – the siren of a police car arriving at Leidse square. A little further up sounds get “neutral”, it's the close-by restaurant ambience.*

Good and bad sounds make us ready for action in different ways. While the sound of music can make you stop to listen to carefully, the sounds of people shouting and yelling at each other make you avoid getting too close to the scene. At this point, the following two questions need to be addressed: Are motor areas of the brain activated differently when you passively listen to these sounds? And is this excitability modulated differently when listening to these sounds with the right, the left or both ears?

It is believed that both hemispheres of the brain receive sounds from each ear, but a great part of the signal from left ear projects to the right hemisphere and vice versa. Each hemisphere is responsible for processing different types of sound information. Models of emotional asymmetry convincingly sustain the existence of distinct processes for emotional encoding within the two halves of the brain. Traditionally, researchers believed the right hemisphere to be more involved in processing emotional information than the left one. Others state that the left hemisphere is specialized for processing positive emotions, whereas negative emotions are lateralized toward the right hemisphere (valence hypothesis). As regards ear laterality in terms of emotions, many studies have in fact reported left ear advantage in recognition of emotional sounds (Haggard and Parkinson, 1971, King and Kimura, 1972, Carmon and Nachshon, 1973, Safer and Leventhal, 1977, Ley and Bryden, 1982, Voyer et al., 2009). In *Chapter 2*, I showed that passively listening to non-verbal emotional sounds, which are presented separately to the left and the right ear, yield differential and possibly lateralized excitability of the corticospinal motor tract (CST). Overall, hand motor area excitability increased in response to unpleasant, as compared to neutral, sounds. Unpleasant stimuli resulted in a higher facilitation of CST in the left hemisphere and pleasant sounds in the right one. Moreover, motor evoked potentials were larger when listening to unpleasant sounds with the left than with the right ear. The facilitation of motor excitability in the left M1 in response to unpleasant sounds, along with the major contribution given by the left ear, suggests the presence of a preference for a direct motor-auditory projection for processing threatening auditory stimuli. This system may have evolved to allow for faster fight-or-flight responses to potential dangerous stimuli.

### **What we do influences what we hear**

*You close your eyes and listen to the sounds around you. People talk; they come closer and disappear. You try to focus on the voice of one speaker talking in one of the languages you know and try to catch a few words. Just for fun, you pick the one that you are sure you cannot completely make out what is being said. You open your eyes; you see that person and look at the mouth. And voilà, all of a sudden you can understand much more of what is being said.*

This Gedankenexperiment shows that what you see can influence what you hear. But does what we do influence what we hear as well? Where and how does this integration of different sensory modalities happen in the brain? The brain receives a continuous stream of information from different sensory modalities. Proper integration of input is essential for accurate perception. Seminal for this is the perception of speech sound, which is clearly affected by observation of facial motion, referred to as the McGurk effect (McGurk and MacDonald, 1976). The perception of the sound of a syllable can also be affected by silent articulation of speech sounds (Sams et al., 2005, Mochida et al., 2013, Sato et al., 2013). *What we do influences what we hear!* In *Chapter 6*, I sought to replicate both visual McGurk and the effect of silent articulation of syllables. I also made an attempt to search for its neural correlates using EEG. As expected, perception of sounds diminished when incongruent syllables were observed and when silently articulated, albeit to a lesser degree. This was accompanied by significant amplitude modulations in beta frequency band in superior temporal areas. The superior temporal sulcus/gyrus (STS/STG) has repeatedly been reported to be involved in the McGurk effect (Calvert et al., 2000, Jones and Callan, 2003, Sekiyama et al., 2003, Bernstein et al., 2008, Irwin et al., 2011, Nath and Beauchamp, 2012, Szycik et al., 2012, Erickson et al., 2014). In this area, event-related beta activities during congruent conditions were phase locked to responses evoked during the auditory only conditions. Our results corroborate these findings, suggesting that STG plays a role not only for audiovisual, but also for audiomotor speech integration.

### **Sounds of silence**

*On your way back to your bicycle, you see two young deaf sisters standing in front of a shop and communicating using a sign language. You can guess what their hands are “talking” about, so to speak, but you do not know the specific word attached to each gesture. You imagine knowing the meaning of some, but not all, of the gestures used. While watching them, you wonder how this kind of communication is processed in the brain. “Do you hear the sounds of silence?” or “Does the brain process the gestural and speech signals in a similar way?”*

Perception of speech and gestures engage common brain areas. Neural regions involved in speech perception overlap with those involved in speech production in an articulator-specific manner. Yet, it is unclear whether motor cortex also has a role in processing communicative actions like gesture and sign language. In *Chapter 3*, I asked whether the mere observation of hand gestures, paired and not paired with words, may result in changes in the excitability of the hand and tongue areas of motor cortex. We found higher motor excitability in the tongue area during the presentation of meaningful gestures (noun-associated), as opposed to meaningless ones, while the excitability of hand motor area was not differentially affected by gesture observation. Taken together, the involvement of the tongue region of M1 is not limited to the perception and production of speech but has a generic role in encoding linguistic (maybe related to phonological retrieval) information even during perception of actions paired with words. The perception of sign language may thus require similar neural activity in speech motor centers as speech perception does.

### **Concluding remarks and future outlook**

During your stay in the Dam Square, you first closed your eyes and localized the band members at different positions. It turns out that some known auditory cues aid auditory localization in humans. Then, the baseball cap of the guitarist made you wonder what sorts of auditory information allow the players of ‘beep baseball’ to anticipate the ball’s arrival? As said, I showed how a simple variable, here the ITD, could serve to intercept a laterally moving sound object properly. However, interacting with a sound source that moves in three-dimensional space may involve other acoustic variables as well. As of yet, we cannot fully address the following question: Which sorts of auditory information are used by beep baseball players to anticipate the path of the beeping ball? Future research should establish how visually impaired people use different acoustic variables, combined or in isolation, for guiding movements so as to interact with a traveling sound source.

On the Dam Square, you tapped your foot with the rhythm’s beat. You asked yourself: Was my movement to the rhythm also influenced by some non-temporal characteristics of music such as pitch relationships? And: Was tapping my foot at the same tempo af-

ter the music stopped playing affected by what I had listened to before? Answering these questions taught us about consonant/dissonant musical intervals and their differences at perceptual and neural levels. I showed that in addition to the rhythm, non-temporal aspects of music could also affect movement timing and form; the movement performance made after exposure to a consonant, as opposed to a dissonant, was found to be different in terms of both timing and form. In-depth knowledge of why consonant musical pitch intervals can benefit the synchronization of movement compared to their dissonant counterparts might enable us to use them as auditory guides to improve movement performance in patients with sensory-motor deficits such as in Parkinson's disease.

During the stroll in Amsterdam, we first categorized all the sounds we heard based on their emotional content and noticed the non-trivial relationships between action preparedness and emotional processing. Then we asked: Are motor areas of the brain activated differently when we passively listen to these sounds? And: Is this excitability modulated differently when listening to them with the right, left or both ears? It turned out that listening to emotional sounds result in differential modulation of excitability of motor cortex dependent on the emotional valence of the sound and the hearing ear. Future research should be devoted to investigating the neural mechanisms underlying this asymmetry.

You closed your eyes and listened to the sounds around you and tried to catch some out of all that were being said. Then you opened your eyes and noticed that observing the mouth of the speaker improves your speech perception. You further asked: Does what I do influence what I hear as well? And: Where and how does this integration of different sensory modalities happen in my brain? The perception of speech sounds can be influenced by both the observation of facial motion and, to a lesser degree, by the silent articulation of speech syllables. Both audiovisual and audiomotor speech integration may happen in the superior temporal areas. Future studies should address this by using neuroimaging techniques with higher spatial resolution, tackling not only the integration of auditory and visual input, but also that of motor information.

Back to the bar where you paid for your drink and the bartender showed you a 'thumbs up'. You knew what that gesture meant. Later, you saw two deaf sisters standing in front of a shop and communicating with sign language, and you imagined to know the

meaning of some, but not all, of the gestures used. You finally asked: Does the brain process the gestural and speech signals in a similar way? The perception of sign language seems to require similar neural activities in speech motor centers as speech perception does. Future work should address whether the excitability in the tongue area of primary motor cortex is merely a function of sign language observation or can it be due to the effects of phonological retrieval or covert speech.

In this thesis, I faced the interaction between our auditory and motor systems from different viewpoints and employed tasks that can be considered to be simple. Evidently, the integration of auditory-motor system is capable of handling complex behaviors such as audiomotor skill learning among musicians and visually impaired people. I trust that understanding the neural foundation of the thoroughgoing integration of sound perceptions and motor actions will certainly help advance this field. Undoubtedly, the variety of the motor tasks involving both auditory and motor systems will promise research topics for the years to come.

*Nothing has been stolen. You are leaving Amsterdam on your bike. You still have your bell but there is no need to use it. You are off center heading south. It is quiet, very quiet – and you have all the time in the world to digest the sounds you heard and start dreaming ... ☺*

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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 extent 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 gebied 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. Beïnvloeden 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 contralaterale 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 werden 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 identificatietask 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 identificatietask 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 verstoort en kennelijk is deze fase, oftewel de timing van het beta-ritme, van belang om verschillende sensorische inputs goed te integreren.

In de epiloog (*Hoofdstuk 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 neurale 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.

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