The orienting response and the motor system

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DISSERTATION

The orienting response and the motor system

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Jeroen Stekelenburg

The orienting response and the motor system

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PROEFSCHRIFT

ter verkrijging van de graad van doctor
aan de Katholieke Universiteit Brabant,
op gezag van de rector magnificus, prof. dr. F. A. van der Duyn Schouten,
in het openbaar te verdedigen ten overstaan van
een door het college voor promoties aangewezen commissie
in de aula van de Universiteit op dinsdag 4 juni 2002 om 16.15 uur

door

Jeroen Jan Stekelenburg
geboren op 2 maart 1967
te Heerlen

Tilburg University

Promotor: prof. dr. C. H. M. Brunia
Copromotor: drs. A. van Boxtel

On the cover: The orienting response was already recognized by Rembrandt. In his painting of 1635, the goddess Athena shows a typical orienting response. She is distracted by something that has happened outside the painting. She stops reading, looks up from her book with her mouth slightly opened, holding her breath. Her little finger seems to indicate where she was in the book.

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Dankwoord

Uit empirisch onderzoek (participerende observatie) blijkt dat het voorwoord of het dankwoord het eerste en vaak het enige is wat van een proefschrift wordt gelezen. Waarschijnlijk is dit proefschrift hetzelfde lot beschoren. Dat zou jammer zijn want er wordt een aantal onderwerpen in behandeld waarover u altijd al meer hebt willen weten. Zo geeft het proefschrift antwoord op de vraag waarom mensen vaak boos lijken te kijken als ze iets moeilijk kunnen verstaan of slecht kunnen horen. Ook geeft dit proefschrift een verklaring voor de vraag waaròm iemands mond soms spreekwoordelijk open valt van verbazing. Is uw interesse gewekt, dan wens ik u veel leesplezier.

Dat ik überhaupt uw interesse mogelijkerwijze heb kunnen wekken, heb ik te danken aan een groot aantal mensen. Ten eerste gaat mijn dank uit naar mijn promotor Kees Brunia. Hij heeft het mogelijk gemaakt dat ik aan dit project heb mogen werken. De belangrijkste bijdrage aan het project komt zonder twijfel van mijn copromotor Ton van Boxtel. Zonder zijn inzet en enthousiasme zou het project niet succesvol zijn afgerond. Ton is een wetenschapper pur sang, iemand die alles tot op het bot wilt uitzoeken. Ook met mij heeft hij de wetenschappelijke discussie niet geschuwd. Soms ging dat gepaard met een dusdanige passie dat passerende AIO's dachten dat we ruzie hadden. Niets is minder waar, mijn ervaring is dat Ton altijd discussieert zonder aanzien des persoons. In de wandelgangen wordt deze op zulke wijze gestoelde zeer kritische uitwisseling van gedachten al aangeduid met een nieuw werkwoord: "vanboxtelen" (een compliment lijkt me). Ondanks de serieuze kant van het project hebben Ton en ik ook altijd veel gelachen over de meest uiteenlopende dingen.

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Het AIO-bestaan kan soms vrij eenzaam zijn, in feite run je een eenmansbedrijfje. Daarom is het zo aangenaam dat een heleboel collega's, mede-AIO's en kamergenoten

mij gesteund hebben, soms door alleen al aanwezig te zijn. De gezamenlijke lunches met de AIO's waren een welkome afwisseling op het verzinnen van nog meer briljante zinnen voor dit proefschrift. Vast gespreksonderwerp en punt van ergernis was de soep: "Hoe is de soep?" Hoe vaak hebben we het bindmiddel in de gebonden tomatensoep niet vervloekt, of het "vlees?" in de groentesoep. En waarom is er alleen erwtensoep in de winter? Ook oplossingen voor de lange rijen voor de kassa zijn veelvuldig besproken. Mochten we met z'n allen mislukken in de wetenschap, dan ligt er nog altijd een glanzende carrière als manager in de horeca in het verschiet. Ik bedank, in alfabetische volgorde: Annekee, Annelies, Antje, Cor, Ellie, Frank, Geertje, Gerda, Gertie, Gilles, Helen, Herman, Ilja, Ingrid, Karen, Karin, Koen, Maaike, Marcel, Marco, Mark, Marlies, Marloes, Michelle, Monique, Onno, Romke, Wery en Wim. Als ik iemand ben vergeten, alvast sorry!

Last but not least gaat mijn dank uit naar Sandra, het licht in mijn leven. Zij stond aan de basis van dit proefschrift omdat zij mij "liefelijk aanspoorde" om op deze AIO-plaats te solliciteren. Ik ben haar voor eeuwig dankbaar. Zonder haar was ik nu waarschijnlijk nog steeds doctorandus! Mijn AIO-periode heeft gedurende een aantal jaren haar AIO-periode overlapt. Het spreekwoord "twee AIO's op één kussen, daar slaapt de duivel tussen" is bij ons echter nooit van toepassing geweest. Met veel geduld, liefde en vertrouwen heeft ze me al die tijd bijgestaan. San, ik kan nu met recht zeggen: "Het is af, eindelijk."

Contents

Chapter 1

General introduction

1.1 Introduction

Being concentrated at work implies giving voluntary selective attention to relevant elements in the environment only, in relative isolation from the rest of the environment. A sudden unexpected change in that environment, for example a birdcall, evokes an orienting response (OR). Attention is shifted from the task at hand to the birdcall. In other words, the active (voluntary) attention is replaced by passive (involuntary) attention to the novel stimulus. So, due to the sudden unexpected change in the environment, ongoing behavior is interrupted to investigate the new stimulus. Pavlov (1927) was the first to study the OR (in dogs) and called it the "What-is-it? response." Sokolov (1963) elaborated on Pavlov's work and described the OR as a complex of nonspecific behavioral and physiological responses to an unexpected, sudden change in environmental stimuli, leading to an increase in alertness and attention. According to Sokolov (1969) the functional significance of the OR is to increase the analyzer sensitivity, resulting in the facilitation of the uptake, transmission, and analysis of environmental information. It is nonspecific in the sense that its elicitation is independent of the stimulus modality. Behavioral and physiological responses include interruption of ongoing activity, directing the sensory organs to the stimulus, heart rate deceleration, an increase in electrodermal activity, and EEG desynchronization. Sokolov claimed that the OR is a complex reaction of the whole organism or a unitary system, implying a covariation of all physiological measures of the OR. This notion, however, has frequently been questioned. Vegetative, somatic, electroencephalographic, and sensory responses exhibit loose or no intercorrelations in OR experiments (e.g., Barry, 1977).

One of the most important defining characteristics of the OR is its habituation induced by repetition of identical stimuli. The attentive behavior, initially evoked by the novel stimulus, diminishes in strength and ultimately disappears when the individual is repeatedly exposed to the same stimulus. Habituation can be considered a basal form of neuronal plasticity and can be described as learning that a stimulus no longer has biological significance. Note that habituation is a hypothetical process underlying overt response decrement. Observed response decrement can be considered habituation only if it cannot be attributed to sensory adaptation, effector fatigue, or infringement of neuronal refractory periods. Habituation is the result of the loss of intrinsic salience of the novel stimulus. According to Thompson and Spencer (1966), to differentiate habituation from fatigue or sensory adaptation, response decrement must be accompanied by response recovery to a deviant stimulus and dishabituation of responses to the subsequent renewed presentation of the habituated stimulus (i.e., enhancement of responses in comparison with those elicited by the last habituation stimulus). Reappearance of the OR to a change in stimulation would be impossible if response decrement is solely the result of sensory adaptation, fatigue, or neuronal refractoriness. Rather, the change in the environment restores the intrinsic salience of the stimulus.

As stated above, Sokolov (1960, 1963, 1969) suggested that the functional significance of the OR is to increase sensory sensitivity. In this opinion, motor effects of the

OR subserve the enhancement of analyzer sensitivity. The ongoing activity is stopped and overt orienting is initiated toward probable sources of future significant stimuli (Kahneman, 1973). Alternatively, other authors claim that the OR prepares the organism for future action or that it constitutes a general preparation to respond (e.g., Germana, 1968; Ruttkay-Nedecky, 1967). However, as asserted by Spinks and Siddle (1983, p. 262) "there is no *a priori* reason to expect that, if orienting facilitates perception, it should also facilitate response systems." Accordingly, the debate is whether the primary locus of effect of the OR is sensory, motor, or central (Rohrbaugh, 1984). This issue has remained unresolved because of insufficient scientific data on motor behavior during the OR. Attention for the motor components of the OR in typical OR experiments has been limited (Barry, 1990; Sokolov, 1963). This thesis concentrates on the changes in the motor system during the temporal course of the OR, using paradigms that have yielded reliable autonomic and central indices of the OR in earlier research. This study could be viewed as an attempt to explore the motor manifestations of passive, involuntary attention.

1.2 Outline of the thesis

The outline of this thesis is as follows. The *theoretical* part consists of three chapters. First, the predominant theories of the OR are reviewed in chapter 2. Chapter 3 reviews earlier studies pertaining to brain manifestations of the OR. Chapter 4 reviews data collected on motor manifestations of orienting. The *experimental* part of this thesis consists of three chapters. Chapter 5 studies changes in the motor system during the OR by evoking Achilles tendon reflexes after presentation of auditory stimuli. It is questioned whether stimulus related changes in reflex amplitude can be taken as an index of the hypothesized preparatory function of the OR. Chapters 6 and 7 focus on the question whether changes in motor activity subserve enhancement of analyzer sensitivity. In chapter 6, the relationship between pericranial (facial) muscle activity and auditory sensitivity is studied. It is hypothesized that inhibition of muscle activity of certain pericranial muscles improves auditory sensitivity. Chapter 7 investigates pericranial muscle activity during nonsignal, OR-eliciting stimuli. It is hypothesized that if the functional significance of the OR lies in the enhancement of analyzer sensitivity and if inhibition of pericranial muscle activity indeed improves auditory sensitivity, orienting to novel auditory stimuli may be accompanied by inhibition of pericranial muscle activity to facilitate the processing of the OR-evoking stimulus. Finally, chapter 8 summarizes and discusses the most relevant findings of this thesis.

Chapter 2

Theories of the orienting response

2.1 Distinguishing between the orienting, defensive, and startle response

Before discussing the relevant theories of the OR, the issue that stimuli can also evoke other involuntary responses than an OR will be addressed first. It is important to take notice of these different responses because they differ in their functional significance. Sokolov (1963) made a distinction between the OR and a second generalized response, the defensive reflex (DR). This distinction was based on different responses elicited by different physical stimulus characteristics. Particularly, stimulus properties like intensity, duration, and rise time affect autonomic responses differently with respect to the direction of the response and its habituation. Sokolov found that stimuli of moderate intensity elicit heart rate deceleration that shows habituation, whereas loud stimuli elicit heart rate acceleration that does not habituate. In Sokolov's opinion, and in accordance with Lacy (1959), cardiac deceleration is associated with sensory facilitation and cardiac acceleration with reduction of sensitivity to sensory inputs. Because of these findings, the OR is believed to be a response reflecting stimulus intake or stimulus approach. The DR is assumed to reflect stimulus rejection or withdrawal from (painful) stimulation.

Experimental data on the effect of auditory stimulus parameters such as intensity, duration, and rise time on autonomic response patterns accumulated in a psychophysiological model that discerns four responses: the OR, DR, Startle Reflex (SR), and Transient-Detecting Response (TDR) (Graham, 1979; Graham & Clifton, 1966). This model is mainly based on heart rate changes because, according to Graham, heart rate is the most reliable autonomic measure to differentiate the OR from the DR. Low intensity auditory stimuli can elicit either a TDR or an OR. Brief, transient stimuli cause a TDR that is characterized by a brief heart rate deceleration with a rapid onset that slowly habituates to identical stimulus repetition. A TDR is sensitive to stimulus onset or change, but not to steady-state stimulus characteristics. It reflects registration but not necessarily identification of the stimulus (Graham, 1992). Stimuli evoking an OR elicit a longer lasting heart rate deceleration that shows habituation to repeated presentation of identical stimuli. In contrast to the TDR, the OR is associated with both stimulus identification and discrimination. Responses to high intensity stimuli can be divided into SRs and DRs. Both the SR and DR are identified by cardiac acceleration. The SR is elicited by brief, transient, high-intensity stimuli with fast rise times and is characterized by a short-latency habituating response component. The DR is elicited by high-intensity, sustained stimuli and is characterized by a longer-latency nonhabituating response component.

Graham (1979) maintained that on the basis of rise time and stimulus intensity there is a strict boundary between orienting and startle. However, this boundary appears to be more fuzzy than originally proposed by Graham, because different studies showed that a cardiac OR turned into a cardiac startle under varying stimulus conditions (Turpin, Schaeffer, & Boucsein, 1999). In some studies stimuli elicited cardiac startle and startle eyeblinks even when stimulus intensity was rather moderate (Blumen-

thal & Goode, 1991; Turpin et al., 1999; Turpin & Siddle, 1983). Turpin et al. (1999) questioned whether in the auditory modality it is necessary to identify a DR in addition to startle. They argued that the early (1–2 s poststimulus) accelerative and late accelerative component (3–6 s poststimulus) of the cardiac response represent two separate components of the startle reflex. The early component is primarily influenced by rise time, whereas the late component is sensitive to the overall intensity of the stimulus.

Cook and Turpin (1997) also disputed Graham's model. They argued that the distinction between different response patterns cannot be solely attributed to the *physical* features of the stimulus. Instead, they hypothesized that stimulus *novelty* or *significance* is important in eliciting responses to transient or sustained stimuli. Graham's model fails to take into account the affective content or the signal value of the stimulus. Studies on the effect of affective pictures on autonomic measures address the question whether aversive pictures elicit either DRs, characterized by cardiac acceleration because of stimulus rejection, or ORs because of the novelty of those pictures. A common finding is that aversive pictures elicit cardiac deceleration, suggesting increased attention (i.e., an OR) to these pictures (Cook & Turpin, 1997). However, when subjects with specific phobias were selected, the aversive pictures related to these phobias elicited cardiac acceleration. In other words, stimuli posing potential personal danger caused a DR. The affective content of pictures also influenced startle eyeblinks that were elicited during or after presentation of the stimulus (Bradley, Cuthbert, & Lang, 1999). Rationale for eliciting startle eyeblinks as a probe is that startle eyeblink modification can, among other things, reveal (the neural mechanisms underlying) cognitive processing of the leading (prepulse) stimulus. As with cardiac responses, startle eyeblink potentiation depends on the specific fear that subjects have for certain aversive pictures. Only fearful subjects showed enhanced startle eyeblinks to aversive pictures compared to neutral pictures (Cook et al., 1992). Thus, it seems that besides the physical stimulus properties, the perception whether stimuli are novel or threatening determines autonomic outputs as well.

2.2 Comparator and noncomparator theories of orienting

The OR literature debates whether synaptic depression and facilitation govern the OR and its habituation or whether elicitation and habituation of the OR require a cognitive process in which a prediction is made about future stimulation based on previous stimulation. Two major theories dominate the debate on this issue, namely the dual-process theory formulated by Groves and Thompson (1970, 1973) as a representative of a noncognitive theory, and a cognitive theory known as the model-comparator theory of Sokolov (1960, 1963). The validation of both theories is primarily based on studies on response decrement, recovery, and dishabituation of autonomic response measures, especially skin conductance response (SCR) and heart rate. The most commonly used design in these experiments is the habituation paradigm. In this paradigm, a number of identical stimuli are presented with rather large interstimulus intervals varying from

some tens of seconds to several minutes. Determinants of the OR may be manipulated, for example, stimulus intensity, stimulus duration, signal value, interstimulus interval, sequential, and probabilistic properties. Generally, it is investigated whether these manipulations affect the absolute magnitude of the OR and/or the rate of response decrement. To study recovery of the OR, a repetition-change paradigm can be employed. The repetition-change paradigm includes a trial at the end of the habituation sequence that is in one or more respects different from the habituation stimulus. The change can constitute the physical properties of the change stimulus, for example, intensity, pitch, duration, hue, shape of visual stimuli, stimulus modality, and so on. In some studies the change was an unexpected omission of the stimulus in a habituation series. Higher order change stimuli have also been used, like change in word meaning. To study dishabituation, a dishabituation trial complements the repetition-change paradigm, that is, the habituation stimulus is presented again after the change stimulus. It is beyond the scope of this thesis to present a detailed review of the antecedents of habituation, recovery, and dishabituation of the autonomic nervous system (ANS) OR. For an extensive review on this subject the reader is referred to Siddle (1983). Also, in chapter 3 some experiments will be discussed that have recorded autonomic measures in addition to central measures.

The next two subsections are devoted to the dual-process theory and the model-comparator theory. Furthermore, section 2.3 discusses which of both theories can best account for the experimental data. Finally, this chapter concludes with a review of more recent cognitive theories of the OR.

2.2.1 Dual-process theory

The dual-process theory is based on spinal reflexes in the hindlimb of the acute spinal cat. In the experiments of Thompson and Spencer (1966), the hindlimb flexion reflex (measured as the contraction strength in the tibialis muscle) of the spinal cat was recorded in response to repeated shocks. The hindlimb flexion reflex decreased as a result of repeated shocks. A change in stimulation resulted in a larger response to the subsequently presented habituation stimulus compared with the previous established habituation level. The stimulus change entailed either an increase in the rate of the presentation of the shock or an intensity increase coupled to an increase in presentation rate, or a natural stimulus, that is, a pinch. The parametric characteristics of the habituation of the spinal hindlimb flexion reflex (Groves & Thompson, 1970) exhibited similar characteristics as the habituation in the intact organism. Therefore, the synaptic organization of the spinal cord was chosen as the model system to study the habituation of the OR (Groves & Thompson, 1970).

According to the dual-process theory, two independent neural mechanisms are responsible for the elicitation and habituation of the OR. As stated in section 1.1, a distinction must be made between overt response decrement and the underlying process of habituation. In the dual-process theory, response decrement is the result of the inter-

action between two inferred, independent processes of habituation and sensitization. Groves and Thompson (1970) postulated two different interneurons (type H and S, see Figure 2.1). In the first process, the inferred intrinsic habituation occurs in the stimulus response (S-R) pathway via the H (habituation) neurons as a result of repeated stimulation. In other words, type H neurons habituate because of synaptic depression induced by iteration of the same stimulus. The inferred habituation generalizes to stimuli that share common elements with the S-R pathway stimulated.

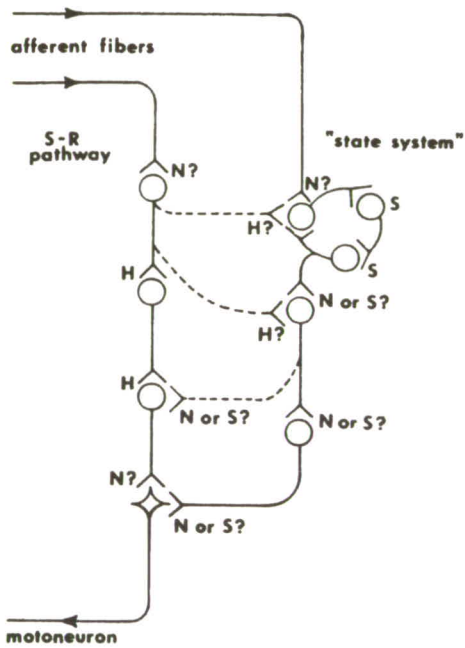

Figure 2.1. Dual-process theory. Schematic diagram of possible neural substrates of habituation and sensitization. N indicates nonplastic sysnapses; H indicates habituating synapses; S indicates sensitizing synapses (adapted from Groves & Thompson, 1970).

In the second process, every stimulus activates an extrinsic sensitization in the S (sensitization) synapses in the nonspecific or state system, which operates independently from the inferred habituation. OR-evoking stimuli raise the general level of excitation of the organism. With moderate stimulus intensities, sensitization first grows and then decays as a function of repeated stimulation. Like inferred habituation, inferred sensitization generalizes to stimuli that share common features. The behavioral outcome, that is, the response to (iterative) presentation of novel stimuli, depends on the competition between the mechanisms of inferred habituation and inferred sensitization.

Response recovery to a deviant stimulus, presented after the habituation stimuli, is explained by incomplete generalization of habituation. The magnitude of response recovery increases with a decreasing overlap between the elements stimulated by the habituation and the deviant stimulus. Dishabituation takes place because of a temporary masking of the inferred habituation by a superimposed sensitization process.

2.2.2 Model-comparator theory

Sokolov (1960) elaborated on Pavlov's conception of the OR in a cognitive OR theory: the model-comparator theory. The core of Sokolov's model is the premise that the magnitude of the OR is determined by the outcome of a comparison between the incoming stimulus and a neuronal model of expected stimulation (Sokolov, 1966). Sokolov (1963, p. 286) defined the neuronal model of the stimulus as a "certain cell system whereby the information is stored concerning the properties of a stimulus which has been applied many times." The model contains information about all the physical, temporal, and higher order aspects of the stimulus and serves as a template for the comparison of new input. The neuronal model can be considered as a prediction of future stimulus events. An OR is evoked when there is a discrepancy between the incoming stimulus and the internally held neuronal model of previous stimulation (Sokolov, 1960, 1963). The magnitude of the OR is directly related to the degree of the mismatch between current stimulation and previous stimulation (Sokolov, 1960).

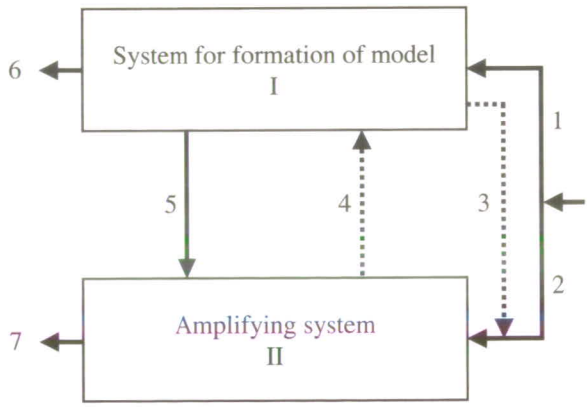

Figure 2.2. Sokolov's model of the orienting response (adapted from Sokolov, 1960).

The model-comparator model (Figure 2.2) assumes that the sensory input follows two pathways: via the specific sensory pathways (1) to the cortex (I, where a neuronal model of the stimulus is build up) and via collaterals of the specific sensory pathways (2) to the mesencephalic reticular formation (MRF: II in Figure 2.2). The information of a novel stimulus will activate the MRF via cortico-reticular pathways (5) and collateral

pathways (2), either because of a mismatch between the present stimulus and the neuronal model of previous stimulation, or because there is no existing neuronal model in case of the very first stimulus in a sequence. The output of the MRF consists of the autonomic and somatic components of the OR (pathway 7) and activation to the cortex (pathway 4). Pathway 6 represents the specific behavioral responses that are transmitted via the specific pathways. The MRF is called the amplifying system because it is believed to have an activating influence on the discriminatory power of the modeling system in the cortex (via pathway 4). Iteration of identical stimuli leads to the build-up of the neuronal model of the stimulus. The formation of the neuronal model inhibits pathway 2 via pathway 3 in Figure 2.2. Inhibition is merely possible if it is assumed that the transmission of information via the specific sensory pathways to the cortex and from the cortex to the MRF is faster than the transmission of information via the nonspecific collateral pathways. As a result of this inhibition, the output of the MRF declines and the OR habituates. When a novel stimulus is presented, the inhibition of the sensory input via the collaterals is omitted and the OR reappears (recovery).

According to Sokolov, the OR is a response to information conveyed by the stimulus. When a novel stimulus is presented, uncertainty is introduced which in turn elicits an OR. The occurrence of the OR facilitates the extraction of the information from the stimulus. Repetition of identical stimuli feeds the information to the neuronal model. With repeated stimulation, the uncertainty and the need for information of the stimulus are reduced. As a consequence, the magnitude of the OR will also be reduced. Because Sokolov's theory is based on information processing, specific predictions can be made. For example, assuming that the rate of habituation of the OR reflects the rate of adding information to the model, habituation of the OR should be rapid to simple nonsignal stimuli and slower to stimuli that are more difficult to model or to discriminate (Graham & Hackley, 1991).

At the time Sokolov proposed his theory, no direct empirical evidence was available for the existence of the neuronal model that was thought to be developed in the neocortex. Two reasons for the lack of evidence can be pointed out (Näätänen, 1992). First, the measures that were used at that time were too slow for tracing fast cerebral processes initiating the OR. For example, the peak latency of SCR ranges from 1 to 5 s after stimulus onset (Levinson & Edelberg, 1985). Second, those measures were too diffuse or nonspecific, making it impossible to pinpoint the involvement of the different central processes. Therefore, animal studies were conducted in which single unit responses were recorded from different brain structures of rabbits in a repetition-change paradigm (Vinogradova, 1975). It was found that in the hippocampus, neurons responded to any stimulus and that this response decreased with stimulus repetition. Any change in stimulation caused a recovery of the response. The initial idea of Sokolov that the neuronal model is formed in the cortical feature detector neurons was abandoned. Instead, Sokolov (1975) considered the location of the neuronal model to be the neuronal network between the cortical feature detectors and the novelty detectors in the

hippocampus. When a stimulus is presented for the first time, a large number of novelty neurons in the hippocampus are activated. The novelty neurons are connected to the reticular formation in which the OR is generated. When the same stimulus is repeatedly presented, the novelty neurons reduce their firing because of the potentiation of collateral inhibitory interneurons between the feature detectors and the novelty neurons. As a result the reticular formation is no longer stimulated. When a different stimulus is presented, other feature detectors are activated and inhibition is released, which resumes the OR.

Recent developments in neuro-imaging techniques made it possible to localize the brain areas in humans that are involved in the elicitation of the OR. Williams et al. (2000) attempted to elucidate the networks underlying the OR in a functional magnetic resonance (fMRI) study. They presented checkerboard stimuli and measured fMRI activity and SCR simultaneously. The neural activity elicited in relation to stimuli that evoked SCR-ORs was compared to the neural activity to stimuli that did not elicit SCR-ORs. Specific neural activity associated with the occurrence of the SCR-OR was found in the anterior cingulate, hippocampus, and ventromedial prefrontal cortex. These results confirm the involvement of brain areas associated with the generation of the OR that were found earlier with animal, stimulation, and lesion studies (Williams et al., 2000).

2.3 Dual-process theory vs. model-comparator theory

Which of the two approaches toward orienting and habituation can best account for the experimental phenomena like habituation, recovery, and dishabituation? Both theories can explain response decrement either in terms of synaptic depression (intrinsic to synaptic mechanisms) in interneurons of the reflex path itself or in terms of extrinsic inhibition, that is, inhibition or excitation not originating in the reflex path. However, response decrement itself cannot be regarded as the point of controversy in this debate, because response decrement is not equivalent to the hypothesized habituation process. Again, habituation can only be demonstrated when response decrement is accompanied by recovery and dishabituation (Thompson & Spencer, 1966). Differences in predictions of both theories therefore focuses on recovery and dishabituation.

First, recovery is discussed. Although recovery can be accounted for by either synaptic depression or extrinsic inhibition, it is generally acknowledged that orienting to a nonarousing event (e.g., a change in stimulation comprising an intensity decrease, or an unexpected omission of a stimulus in a sequence) poses problems for the dual-process theory (e.g., Graham & Hackley, 1991; Siddle, 1991; Siddle & Lipp, 1997).

According to the dual-process theory, recovery is the result of incomplete generalization of habituation. That is, recovery is determined by the number of "fresh" elements of the deviant stimulus that is not shared with the habituation stimulus. High intensity stimuli will activate almost all elements, whereas low intensity stimuli will activate relatively fewer elements. Stimulus omission will not activate any fresh elements.

When the intensity of the habituation stimulus is low relative to the deviant, recovery will be large because a lot of elements activated by the deviant will not have been habituated. A stimulus change involving an intensity decrease would result in either a small or no recovery because only few fresh elements are activated that were not activated by the stronger habituation stimulus (Thompson, Groves, Teyler, & Roemer, 1973).

In the model-comparator theory, recovery is said to be caused by the discrepancy between actual and anticipated stimulation. The model-comparator theory predicts the same magnitude of recovery to either intensity increase or decrease or even to stimulus omission (Sokolov, 1963). To better understand recovery to a stimulus change, Sokolov (1975) specified his theory on a cellular level. He postulated three different types of neurons (see also Figure 2.3):

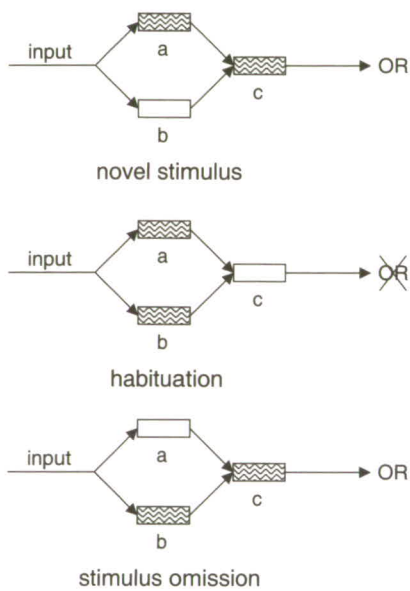

Figure 2.3. Schematic diagram of the functioning of afferent neurons (a), extrapolation neurons (b), and comparator neurons (c) in case of a novel stimulus, habituation, and stimulus omission (after Sokolov, 1975).

a. afferent neurons (always) respond to sensory input;
b. extrapolation neurons receive the same input as the afferent input, but start to fire with repeated stimulation;
c. comparator or novelty neurons respond to the difference between afferent and extrapolation neurons.

A novel stimulus will activate afferent neurons, while at the same time extrapolation neurons will not fire. Comparator neurons will respond because of the maximal diffe-

rence between activities of afferent and extrapolation neurons, and as a result, the OR is elicited. With repeated stimulation, both afferent and extrapolation neurons fire and the difference between them will diminish, hence the OR will decline. In case of stimulus omission, extrapolation neurons are still activated because of previous stimulation whereas afferent neurons are not. An OR is elicited as a result of the firing of the comparator neurons, induced by the difference between the activities of the afferent and extrapolation neurons.

There is some controversy, however, about the fact whether a nonarousing stimulus actually causes the same recovery as an arousing stimulus after a series of stimuli that are less arousing (Siddle, 1983). According to the model-comparator theory, the amount of deviance determines the magnitude of recovery, regardless the direction of the deviant, because of the principle of generalization of habituation. Although significant recovery and dishabituation of the SCR-OR were found in response to a change stimulus of lower intensity than the habituating stimulus (e.g., Rust, 1976), Bernstein (1968) and Van Olst (1971) demonstrated that recovery and dishabituation were smaller in case of an intensity decrease as opposed to an intensity increase. Bernstein concluded that an intensity increase is to be perceived as more significant than an intensity decrease. He argued that an OR is evoked only when the stimulus is relevant enough. An alternative explanation that may account for this differential effect is that besides generalization of habituation the law of strength takes effect. That is, recovery is larger to an intensity increase because louder stimuli in themselves produce a larger response (Sokolov, 1963).

An even stronger test for the dual-process and model-comparator theories are stimulus omission studies, in which in a habituation series a stimulus is unexpectedly omitted. However, stimulus omission studies also produced mixed results. In contrast to the prediction of the model-comparator theory, merely less than half of the subjects showed reliable SCR-ORs to missing stimuli (O'Gorman, 1989; Siddle & Heron, 1975). In short, these studies on recovery to a nonarousing event, interspersed in a series of homogeneous stimuli, do not constitute a decisive argument in favor of either theory.

Evocation of recovery and especially dishabituation to stimulus omission in the paired-stimulus paradigm proved to be a more valuable test for the predictions of cognitive and noncognitive theories of the OR. The paired-stimulus paradigm, incorporates differential predictions of both theories regarding recovery and dishabituation. In the paired-stimulus paradigm, stimulus pairs are repeatedly presented such that the onset of the second stimulus (S2) coincides with the offset of the first stimulus (S1). The question is whether the omission of S2 (after several presentations of S1-S2 pairs) results in recovery of the response to the missing stimulus and dishabituation of the response to S2 when the S1-S2 pair is presented on the next trial after the omission. According to Siddle (1991), the paired-stimulus paradigm is the most crucial manipulation in testing the predictions of comparator and noncomparator theories. The model-comparator theory explains dishabituation in terms of a disruption of the underlying habi-

tuation process. The response to the habituation stimulus presented subsequently to the deviant stimulus is said to be enhanced because the deviant stimulus disrupts the neural model of the habituation stimulus. Therefore, any disruption of the model including stimulus omission should cause dishabituation. The dual-process theory on the other hand suggests that dishabituation is the result of a superimposed sensitization process induced by the deviant stimulus. Siddle (1991), however, finds it difficult to explain dishabituation to stimulus omission in terms of sensitization induced by the absence of stimulation. Dishabituation would be expected only after arousing events. Therefore, according to the dual-process theory, dishabituation is not to be expected after stimulus omission. Thus, both theories have different predictions about the effect of stimulus omission on recovery and dishabituation. Siddle (1985) found recovery of the SCR-OR to the omission of S2. When the S1-S2 pair was presented again after the omission trial, dishabituation of SCR-responses was found to S2 but not to S1. According to Siddle, the dual-process might account for these findings in two ways. First, omission of S2 may have caused the interstimulus interval to be longer, resulting in an enhanced response to the renewed presentation of S2 because of spontaneous recovery. However, in a control condition in which an extra long interstimulus interval between two trials at the end of the habituation training was introduced, no enhanced response to S2 was found. Second, for the sake of the argument, the dual-process theory might argue that omission of S2 somehow results in sensitization. However, in that case one would expect an enhanced response to the subsequent S1 as well, which was never found. Thus, dishabituation cannot be explained by arguing that the omission of S2 produces sensitization that persists until the next trial. The dual-process theory predicts dishabituation only following arousing deviants (Graham & Hackley, 1991). There is nothing to respond to, yet the subject responds. This is only possible if the subject has an internal representation of past stimulus events and a certain expectation of future events.

The results of the stimulus omission studies leave us with the question why with single stimulus presentations, stimulus omission produced no robust recovery and dishabituation, whereas in the paired-stimulus paradigm, stimulus omission typically evoked recovery and dishabituation. Siddle and Lipp (1997) considered expectancy to play a central role in this differentiated effect of stimulus omission. They argued that with repeated presentation of S1-S2 pairs, S1 becomes a good predictor of S2. Indeed, the expectancy of S2, indicated by the subjects in an experiment of Siddle, Booth, and Packer (1987), rose as a function of the number of trials. Omission of S2 is unexpected and weakens the relationship between S1 and S2. When subjects had to indicate the certainty whether S2 would occur on the next trial, expectancy of S2 after omission of S2 dramatically decreased (Siddle et al., 1987). Renewed presentation of S2 on the next trial is in itself a surprising event that causes an OR. If expectancy determines the effect found in S1-S2 paradigms, one would expect this effect to be larger after more habituation trials. Siddle, Lipp, and Dall (1996) demonstrated that the SCR-OR to an intermodality change was larger after 24 training trials compared to 6 training trials. These

results seem to suggest that expectancy develops during habituation training and that violation of the expectancy evokes orienting. Thus, it appears that cognitive factors such as expectancy instead of noncognitive factors such as synaptic depression and facilitation play a role in the elicitation and habituation of the OR.

According to Graham and Hackley (1991), the strongest evidence in favor of cognitive theories, in addition to the paired-stimulus experiments, comes from studies in which higher order stimulus factors were varied. For example, insertion of an out-of-sequence digit, a change from an alternating to a repeated pattern, and even changes in word meaning can produce recovery of OR components. These results strongly support cognitive theories of the OR (Graham & Hackley, 1991).

In summary, the dual-process theory can account for habituation of low-level reflexes. However, as demonstrated in this section, it has proven to be difficult to consider the mechanisms of synaptic depression as the basic process underlying habituation. Experimental data on stimulus omission and higher order changes suggest that the subject develops some expectancy of the stimulation. Therefore, sensory events must have an internally held representation that enables extrapolatory processes in which future events are anticipated. It is the model-comparator theory that has incorporated cognitive conceptions of representation and the capacity of extrapolation.

Although it is generally acknowledged that the model-comparator theory does a better job in explaining experimental data on the OR, some investigators questioned the validity of the theory. Criticisms pertained to two issues. First, in the model-comparator theory, Sokolov made no distinction between the OR evoked at the beginning of a stimulus sequence and the OR evoked by stimulus change. In both cases the neuronal model is lacking. O'Gorman (1979) objected to the notion that both initial stimulus presentations and stimulus change lead to the same OR. He therefore made a distinction between the initial orienting response and the change orienting response. This distinction will be elaborated upon in section 3.6.1. Second, Bernstein (1969) doubted whether the novelty of the stimulus is sufficient to elicit an OR. Bernstein asserted that only a change in the environment that is both novel and significant for the organism, leads to an OR. The issue of stimulus significance will be addressed in sections 2.4 and 3.6.2. Note that in OR literature and in this thesis the terms stimulus significance and stimulus relevance are used interchangeably.

2.4 Elaborations on the model-comparator theory: The role of significance

In OR literature it has been debated whether stimulus novelty is a sufficient condition in eliciting an OR or whether the stimulus should also have some significance to the individual. According to Sokolov (1963), the slightest change in the environment should evoke an OR. A number of studies contradicted this prediction because a change in stimulation failed to produce an OR in all subjects (e.g., Bernstein, 1969). Bernstein (1981) concluded that the incidence of nonresponsiveness to a stimulus change ranges between 40–60%. The prediction of the model-comparator theory that a change in

intensity of the stimulus, irrespective of the direction, would elicit an OR, could not be demonstrated by Bernstein (1968). The intensity increase had a larger effect on the OR than the intensity decrease. Bernstein et al. (1971) provided additional evidence against this specific prediction of the model-comparator theory. They conducted an experiment in which the response to an apparently moving visual stimulus was studied. It was found that stimuli apparently moving toward the subject elicited a stronger OR than stimuli apparently moving away. Bernstein accounted for these results by arguing that an intensity increase, as well as an object moving toward someone, gives the impression of something approaching and is therefore significant. Other studies have been conducted in which stimulus significance has been experimentally manipulated in a number of ways, including counting of stimuli, subjective ratings of subjective impact, perceptual judgments, and overt responses (Rohrbaugh, 1984). Bernstein argued that a stimulus change per se is not enough to elicit an OR. Subsequent to the detection of the stimulus change there is a stage in which the meaning or relevance of the stimulus is evaluated. Only if the stimulus is relevant enough, an OR is elicited. In line with Bernstein, Kahneman (1973) proposed a multiplicative interaction effect of the factors novelty and significance on the OR. Only when both conditions are met an OR is evoked.

Siddle (1979) and O'Gorman (1979) rejected Bernstein's multiplicative nature of the relationship between stimulus change and stimulus significance. Instead, they argued that this relationship is additive. Experiments in which novelty and significance were simultaneously manipulated demonstrate that both factors had an additive effect on the SCR-OR (Ben-Shakhar, 1994; Gati & Ben-Shakhar, 1990; Siddle, O'Gorman, & Wood, 1979).

The model-comparator theory cannot account for evocation of the OR by a familiar but significant stimulus (Näätänen, 1979; Öhman, Hamm, & Hugdahl, 2000). Significant stimuli, which are familiar by definition, are incorporated in memory models. The implication is that an OR is elicited by a *match* between the significant stimulus and the memory model instead of a *mismatch*. Öhman (1979) postulated an information-processing model of orienting to reconcile opposite theoretical demands posed by ORs to signal and nonsignal stimuli. The underlying idea of the model is that the OR can be viewed as a call for processing resources in a central, capacity-limited channel. Both signal and nonsignal stimuli evoke a call for central processing. In other words, both stimulus types indicate a need for further information processing of the stimulus. Stimuli are selected by preattentive mechanisms working parallel in order to achieve identification of the stimulus. The preattentive mechanisms do not allocate central processing capacity nor interact with a short-term memory store (STS) that contains contextually activated segments from a long-term memory store (LTS). Öhman's model considers novelty and significance as different psychological processes that may both lead to the same OR. Öhman distinguished two qualitatively different routes in the nervous system, one for task-relevant stimuli (signal OR) and one for nontask-relevant stimuli (nonsignal OR). If there is a mismatch between the outcome of the preattentive

mechanisms and the representation in the STS, a nonsignal OR is elicited and the stimulus is admitted into the central channel. A long-term memory search for associated memory representations is initiated and the stimulus is processed for encoding into the LTS. This is what Öhman called rehearsal. It implies an interaction between the LTS and the STS. Alternatively, a stimulus can elicit an OR via the signal route when it matches a memory representation that has been primed as significant. The stimulus enters the central channel for further processing. In that case, relevant information is retrieved from the STS allowing the initiation of plans for action, including expectations of forthcoming stimuli whose representations are transferred to STS. In his original theory both the call for processing resources and the associated OR were assumed to have a preattentive origin. On the basis of experiments with masked stimuli in which it was assured that stimuli could only be processed at the preattentive level Öhman (1992, 1993) revised his model. The modifications implied that only ORs to biologically significant stimuli have a preattentive origin, whereas ORs to nonsignal stimuli reflect controlled processing.

Ben-Shakhar and colleagues introduced the feature-matching model in which two independent factors, that is, novelty and significance, determine the elicitation of the OR (Ben-Shakhar, 1994; Gati & Ben-Shakhar, 1990). As an elaboration on Öhman's model they tried to specify the nature of the matching process that determines these factors. When a sequence of stimuli is presented, each stimulus is compared with the existing representations of significant stimuli and with the neuronal models created by the stimuli preceding it in the sequence. The magnitude of the OR is determined by the novelty value (the degree of its distinctiveness from the preceding stimuli) and the level of significance (its match with representations of significant information).

The next chapter reviews experimental findings on changes in brain activity elicited by novel stimuli. The presented studies show that under different conditions novel stimuli evoke different systematic changes in brain activity. These so-called event-related brain potential (ERP) studies contribute to a better understanding of the underlying neural processes of the OR

Chapter 3

Brain manifestations of the orienting response

3.1 Introduction

Electroencephalography (EEG) has been frequently used in OR research paradigms. Rohrbaugh (1984) claimed that EEG measures, as a central index of the OR, offer a valuable complement to autonomic and behavioral measures. They are dimensionally complex responses that encode unique sorts of temporal and localizing information that is not available in other response systems. Central measures give more direct insight than autonomic measures in processes where the OR is generated: the brain. One of those brain manifestations is the event-related potential (ERP). ERPs provide a powerful tool to investigate the OR. An ERP is an event-related change of brain potentials embedded in spontaneous (random) EEG. Because of this random EEG activity, ERPs are difficult to distinguish in individual trials. The signal to noise ratio (SNR) of a single ERP is very low. To increase the SNR, the averaged ERP of several trials can be computed. Stimulus or event-related EEG that is time-locked will be preserved in this operation, but spontaneous activity will be averaged out. In studying response decrement, averaging of a series of successive trials (or long term averaging, LTA) obviously fails to detect very fast changes, especially when the averages comprise ten or more trials. A potential response decrement could be lost in the average. To avoid this problem, ordinal averaging (or short-term averaging, STA) can be applied. In STA, several blocks of stimuli are presented. The interblock interval is several times the length of the interstimulus interval, allowing the ERP to completely recover. ERPs are then averaged across those stimulus presentations that occupy similar ordinal positions within the different stimulation blocks. Thus, the first trial of each block is averaged, the second trial of each block is averaged, and so on. A potential problem of this approach is that combining early (first trial in first block) and late responses (first trial in last block) may result in an underestimation of the habituation process (Verbaten, 1997). Therefore, a third method to increase SNR has been developed. The orthogonal polynomial trend analysis (OPTA) enables analysis of ERPs on single trial basis (Woestenburg, Verbaten, Van Hees, & Slangen, 1983). ERPs are transformed to the frequency domain. In the frequency domain, an orthogonal polynomial is fitted (up to the fifth order) across several consecutive trials per frequency component. Only significant polynomials are then transformed back to the time domain. Finally, it is also possible to decide *not* to apply any SNR-enhancing techniques, but simply use the raw ERP scores, thereby allowing for maximal noise and variability of the ERP.

Is there a unique ERP component that can be considered a central manifestation of orienting? Or, as Kenemans (1990) put it, is there a full-fledged cerebral OR-component? From ERP-OR literature it has become apparent that there is no sole candidate for being the single central index of the OR, because different ERP components respond differently to OR-manipulations, such as iteration of identical stimuli, stimulus deviation, and stimulus relevance. Yet, three ERP components can be considered indexes of (or are at least associated with) involuntary orienting: N100, mismatch negativity (MMN), and P3. In ERP-OR studies, it has been investigated whether these ERP

components satisfy the properties of the OR. As will become apparent in the review of these ERP components in this chapter, these studies show inconclusive and contradictory results. For example, they differ on the rate and curvature of response decrement, the occurrence of recovery and dishabituation, the influence of stimulus significance on response amplitude and response decrement, and the covariation between habituation of ERP components and habituation of autonomic responses. In some cases, these inconclusive results can be ascribed to the different averaging procedures used. As suggested above, LTA cannot detect fast decrement as is usually found for SCR, especially when the average contains 10 or more trials. Furthermore, ordinal averaging may result in an underestimation of response decrement (Verbaten, 1997). The inconclusive or even contradictory results of these studies should therefore be interpreted with some caution.

3.2 N100

The auditory N100 is a negative brain wave that usually starts around 60 ms and peaks at about 100 ms after stimulus onset. At least three generators contribute to the auditory N100 (Näätänen & Picton, 1987). The first is located in the auditory cortex in the supratemporal plane. The second component (T-complex) originates in the auditory association cortex in the temporal gyrus. The third component is a nonspecific one that reaches its maximum at the vertex. Näätänen and Picton (1987) suggested that the nonspecific component is generated in the frontal motor and premotor cortex under influence of the reticular formation and the ventral lateral nucleus of the thalamus.

Näätänen (1992) reviewed the main determinants of the auditory N100. The N100 potential is evoked by a relatively abrupt change in the level of energy impinging on the sensory receptors. Particularly, the N100 is elicited by stimulus onset and offset. The slope of the energy change (i.e., the rise time or fall time) determines the N100 latency and amplitude. As stimulus intensity decreases, the N100 decreases in amplitude and increases in latency. N100 amplitude increases with stimulus intensity, but levels off at high intensities. Furthermore, there is a positive relationship between interstimulus interval and N100 amplitude. N100 amplitude increases up to interstimulus intervals of about 16 seconds.

Now the question becomes relevant whether the N100 displays the typical OR-characteristics such as response decrement with repeated presentation of identical stimuli, recovery, and dishabituation after presentation of a deviant stimulus. Although recovery and dishabituation are key properties of habituation, most studies investigating habituation of the N100 do not include a dishabituation trial. Therefore, one cannot ascertain whether the observed decrement of the N100 reflects "true habituation" or is the result of some kind of neuronal refractoriness in these studies.

Various manipulations that may affect the amplitude and the decrement of the N100 have been employed. The most varied factors include stimulus repetition, interstimulus interval (ISI), stimulus relevance, and stimulus change. The next three subsections review the results of studies on the habituation of the N100.

3.2.1 The effect of length and regularity of ISI and stimulus intensity on the decrement of the N100 in different modalities

The length and regularity of ISI and stimulus intensity have been shown to affect both the magnitude of the ANS-OR and its habituation (Siddle, Stephenson, & Spinks, 1984). In several ERP studies it was investigated whether these stimulation parameters would also affect N100 amplitude and its habituation.

In STA studies, ISI is usually less than ten seconds. Repeated presentation of identical stimuli at these short ISIs generally yields a fast curvilinear decrement of N100 amplitude (or N1-P2 in earlier studies) in different modalities, reaching an asymptotic level before the third or fourth trial, but often already at the second trial (in the *auditory modality*: Barry et al., 1992; Bourbon et al., 1987; Budd et al., 1998; Donald & Young, 1980; Fruhstorfer, 1971; Fruhstorfer, Soveri, & Järvilehto, 1970; Maclean, Öhman, & Lader, 1975; Megela & Tyler, 1979; Öhman, Kaye, & Lader, 1972; Öhman & Lader, 1972; Ritter, Vaughan, & Costa, 1968; Roth & Koppell, 1969; Woods & Elmasian, 1986; in the *visual modality*: Bruin, Kenemans, Verbaten, & Van der Heijden, 2000; Megela & Tyler, 1979; Wastell & Kleinman, 1980; in the *somatosensory modality*: Fruhstorfer, 1971; Kekoni et al., 1997).

Higher auditory stimulus intensities and longer ISIs result in enhanced N100 amplitude (Öhman & Lader, 1972; Roth & Koppell, 1969). A shorter ISI is associated with a faster response decrement compared to a longer ISI (*auditory*: Budd et al., 1998; Fruhstorfer et al., 1970; Ritter et al., 1968; Woods & Elmasian, 1986, *visual*: Wastell & Kleinman, 1980). With an ISI of ten seconds, Budd et al. (1998) and Ritter et al. (1968) found no decrement of the auditory N100. In the study of Öhman and Lader (1972) the opposite pattern was found. The decrement with repeated auditory stimuli was more pronounced with long ISIs (8–12 s) compared to short ISIs (2.4–3.6 s).

Studies on the effect of regularity of stimulus presentation on the decrement of the N100 produced mixed results. Whereas Öhman et al. (1972) found that the decrement of auditory N100 amplitude in the regular ISI condition was both steeper and more curved than in the irregular ISI condition, in the study of Maclean et al. (1975) irregularity of ISI failed to affect the decrement of the auditory N100.

In LTA paradigms, ISI is usually considerable longer than in STA paradigms, ranging from 12 s (Schandry & Hoefling, 1979) to 33 s (Rust, 1977). The decrement of the auditory N100 is either absent (Schandry & Hoefling, 1979; Simons et al., 1987) or very small (Rust, 1977). In these studies, LTA of 4 trials and more, prohibits the discovery of fast decrement. However, in the study of Simons et al. (1987), the auditory N100 diminished rapidly within the first block of four trials.

In single trial studies using both long and short ISIs, N100/N1-P2 amplitude decreased rapidly as a function of stimulus repetition (to *auditory* stimuli: Experiment 2 of Simons et al., 1987, to *visual* stimuli: Kenemans, Verbaten, Sjouw, & Slangen, 1988; Kenemans, Verbaten, Roelofs, & Slangen, 1989; Woestenburg et al., 1983). In the studies Kenemans et al. (1988, 1989), the visual N100 decreased at the same rate as SCR.

3.2.2 The effect of stimulus relevance on the decrement of the N100 in different modalities

Stimulus relevance can be manipulated in various ways. A procedure that has frequently been used to make stimuli relevant, is to instruct the subjects to count stimuli or to perform a voluntary response. Stimuli can be made stimulus-irrelevant when subjects are instructed not to respond in any way, or by presenting a secondary task to the subjects. In habituation studies, stimulus relevance has affected the absolute amplitude of the N100 and/or the decrement of the N100 across identical stimuli. In general, N100/N1-P2 amplitude is larger to auditory stimuli in a stimulus-relevant condition than in a stimulus-irrelevant condition (Donald & Young, 1980; Maclean et al., 1975; Öhman & Lader, 1972), except in the study of Becker and Shapiro (1980). Stimulus relevance caused a delay of the decrement of the auditory N100 in a study of Barry et al. (1992), but not in the study of Öhman and Lader (1972). Maclean et al. (1975) found a steeper decrement when the attention was directed away from the auditory stimulus, but only when the distracting task involved a low activation level. When, in a subsequent experiment, only attention was varied and not activation level, stimulus relevance did not influence the rate of decrement of the auditory N1-P2 (Maclean et al., 1975). In a study of Kenemans et al. (1988), presentation of stimulus-relevant visual stimuli with a variable ISI of 10–20 s resulted in an enhanced amplitude of the N100 and in a delayed decrement of the N100 at electrode position Oz compared to stimulus-irrelevant stimuli. No task effects were observed at Cz. Stimulus relevance affected SCR in the same manner as the visual N100 at Oz. Kenemans et al. proposed that two different processes could be distinguished: the nonspecific N100 at Cz that is not influenced by stimulus relevance and the occipital N100 that depends on stimulus relevance. Later results of Kenemans et al. (1989) refuted their proposal. Neither the amplitude of the nonspecific N100 nor the amplitude of the occipital N100 were influenced by stimulus relevance when fixed ISIs of 2.45 and 8.45 s were used. Stimulus relevance had also no effect on the rate of decrement of the visual N100. The decrement of SCR was also the same for both conditions. The results of Kenemans' experiments (Kenemans et al., 1988) suggest that only when ISI is variable, stimulus relevance influences the N100. This differential effect was also found in Experiment 1 of the study of Maclean et al. (1975). Stimulus relevance only affected auditory N100 amplitude when ISI was irregular, varying from 2.4 to 3.6 s, opposed to a fixed ISI of 3 s.

In conclusion, the effect of stimulus relevance on the rate of decrement of the N100 has not been well established. Delayed decrement of the N100 to relevant stimuli was only demonstrated by Barry et al. (1992) to auditory stimuli and by Kenemans et al. (1988) to visual stimuli. Second, several studies found larger N100 amplitudes when attention was directed to the stimulus, but in other studies this effect could not be replicated. Variability of ISI probably influences the effect of stimulus relevance on N100 amplitude and the decrement of N100 amplitude.

3.2.3 Recovery and dishabituation of the N100 in different modalities

As put forward earlier, if the decrement of the N100 is a genuine habituation effect, it should be accompanied by recovery and dishabituation. Despite the importance of recovery and dishabituation, only a few N100 studies included a deviant stimulus in a habituation series. Recovery of N100/N1-P2 amplitude was found in several studies (change in *pitch*: Barry et al., 1992; Woods & Elmasian, 1986, change in *geometric form and/or color of visual stimuli*: Bruin et al., 2000; Kenemans et al., 1989, *intermodality change*: Fruhstorfer, 1971). However, the auditory N100/N1-P2 failed to show recovery in the studies of Budd et al. (1998), Ritter et al. (1968), and Simons et al. (1987). Whereas recovery of the auditory N100 was absent in Experiment 1 of the study of Simons et al. (1987), SCR did show recovery. In a study of Megela and Tyler (1979), using visual and auditory stimuli in separate conditions, the N1-P2 recovered only when the deviant stimulus had a higher intensity than the habituation stimulus. This effect was corroborated by Experiment 2 in the study of Simons et al. (1987). Although Simons et al. did not analyze recovery of the auditory N100 explicitly, visual inspection of the ERPs in their Figure 8 suggests a recovery of the N100 to an intensity increase of an auditory deviant. In addition, the loud deviant stimulus induced an increase in electrodermal activity and heart rate deceleration.

Studies on the dishabituation of the N100 component are scarce. Megela and Tyler (1979) found dishabituation of the N1-P2 after both an intensity increase and decrease in auditory and visual modalities. Others were unable to replicate these findings (*auditory*: Barry et al., 1992; Budd et al., 1998, *intermodality change*: Fruhstorfer, 1971). In two instances dishabituation of SCR was observed while the N100 did not display dishabituation. First, in the experiment of Simons et al. (1987) SCR dishabituated to a pitch change. Second, Barry et al. (1993) conducted an experiment in which they studied habituation of the SCR-OR using the same paradigm and the same parameters as Barry et al. (1992). Although the auditory N100 failed to show dishabituation (Barry et al., 1992), SCR demonstrated significant dishabituation (Barry et al., 1993).

In summary, it can be concluded that recovery of N100 amplitude is not a stable phenomenon. The N100 recovers to an intensity increase and to a modality change. When the deviant trial differs only qualitatively from the habituation stimulus (e.g., a different pitch) this does not invariably result in recovery. Part of the problem to demonstrate recovery of the N100 may lie in the use of the STA paradigm. To enhance the SNR, a relative large number of stimulus blocks are presented, usually more than 15-20 blocks. It could be that recovery of the N100 habituates across the blocks, leading to a significant reduction of the magnitude of recovery in the ordinal average. Kenemans et al. (1989) tested this hypothesis. Immediately after a habituation series, presentation of the visual habituation stimulus was continued with insertion of an occasional visual deviant (14 times). Recovery to the presentation of the deviant stimulus was found only to the first few deviants. Recovery of the N100 thus declined with repeated presentation of the deviant stimulus. It might be argued that the failure

to demonstrate recovery is partly the result of generalization of habituation. However, in the Kenemans et al. study, a visual deviance wave was found (P2-N2) that did not decline over trials. Budd et al. (1998) also found a MMN-like deviance wave to an auditory deviant, in the absence of recovery of the N100. These results demonstrate that despite the lack of recovery of the N100, the brain responded to the change in stimulation, ruling out generalization of habituation.

The data on recovery of the N100 seem to suggest that the N100 reflects the initial novelty of the stimulus. Alternatively, the neural generators underlying the N100 might primarily respond to a very large difference between previous stimulation and the current stimulus, such as intermodality changes. Verbaten (1997) proposed that the N100 signals the detection of "outside-channel" events (see section 3.6.1). In section 3.3, an ERP component called the MMN will be discussed that possesses properties that are perpendicular to the N100. Unlike the N100, the MMN is evoked to a change in stimulation only and not to the presentation of the stimulus per se.

Although dishabituation has not frequently been the subject of investigation, most ERP research found no evidence for dishabituation of N100 amplitude. It is not unlikely that dishabituation of N100 amplitude habituates itself, like recovery of the N100, which was demonstrated by Kenemans et al. (1989). To our knowledge, no study has been done on the habituation of dishabituation of N100. Because of the inconclusive results regarding recovery and dishabituation of the N100, there is a dispute about whether the observed decrement of the N100 is a habituation effect or whether it is merely the result of some kind of refractoriness of the neural generators of the N100. The next subsection will continue upon this discussion.

3.2.4 Is there evidence for habituation of the N100?

The data on habituation of the N100 have frequently been discussed, in particular whether the decrement of the N100 reflects "genuine" habituation induced by the loss of novelty (habituation hypothesis), or whether it is the result of neuronal refractoriness (refractoriness hypothesis). Ritter et al. (1968) proposed that the decrement of the auditory N100 with short ISIs could invoke a relative refractoriness within its generators. Although the physiological mechanisms underlying response decrement of the N100 are not known, Näätänen and Picton (1987, p. 400) conjectured that "it is unlikely that they are caused by actual refractory periods in simple cellular mechanisms. Synapses do not usually get tired that quickly or recover that slowly." Näätänen (1992) advanced that the characteristics of the decrement of the N100 would suggest a process involving a refractory period of the polysynaptic neural generators underlying the N100, rather than a process in which the decrement of the N100 is a cerebral manifestation of the loss of novelty mediated by a match/mismatch mechanism. For example, response decrement induced by refractoriness would be completed after the presentation of the second trial and would be stable for the ensuing trials. This has often been observed in the decrement of the N100, instead of the more negative exponential decrease such as

observed in autonomic response measures. On the other hand, other studies (especially the studies of Verbaten and Kenemans) reported that the rate of decrement of the visual N100 was comparable to that of SCR. To demonstrate "genuine" habituation, recovery and dishabituation should occur next to response decrement (Thompson & Spencer, 1966). Not all habituation studies have included a deviant trial, but those who did, produced mixed results as described in the previous subsection. Budd et al. (1998) concluded that recovery of the N100 is not a stable phenomenon. Furthermore, dishabituation is seldom found.

Näätänen (1988, 1990, 1992) provided an alternative explanation for the decrement of the (auditory) N100 (in STA studies). He proposed that the large auditory N100 to the first stimulus in a stimulus sequence mainly originates from a very large nonspecific component. This nonspecific component is not elicited in subsequent trials. The much smaller N100 amplitude in subsequent trials is mainly composed of the supratemporal component. The neural population underlying the nonspecific component triggers a widespread transient arousal burst, facilitating sensory and motor responses (Näätänen & Picton, 1987). This arousal response contributes indirectly to the conscious perception of the stimulus (Näätänen, 1988). According to Näätänen (1990) this generator process cannot subserve conscious perception of auditory stimuli in general because of the long refractory period of this component. The activation of the neural population underlying the supratemporal component of the N100 might be linked with conscious perception in a more direct manner, instead of via an arousal response. The supratemporal component is said to be susceptible to energy change but not to specific information contents (Näätänen, 1988). The function of this generator process is to inform *that* a stimulus has been presented but not *what* stimulus has been presented. It could be considered as an internal attention trigger, facilitating conscious perception of auditory stimuli. The decrement of the auditory N100 might be accounted for in terms of the refractoriness of the specific and nonspecific generators. Näätänen (1992) claimed that refractoriness is to some extent stimulus specific because a deviant stimulus interspersed into a habituation series can result in a (partial) recovery of N100 amplitude. According to Näätänen, this should not be explained in terms of the OR theory, but rather it is the result of the activation of different neural populations activated by the standard and the deviant auditory stimulus (Näätänen et al., 1988). It is believed that this stimulus-specific refractoriness is developed in the supratemporal generator, which has a tonotopic organization (Pantev et al., 1988).

In short, the occurrence of recovery of the auditory N100 per se is not the decisive argument in favor of the habituation hypothesis. It can be equally well explained by renewed novelty or by a refractory process. Additional support for the hypothesis that on the first trial mainly the nonspecific generator contributes to the auditory N100 and the supratemporal component in subsequent trials, came from Pang and Fowler (1997). They presented thirty blocks of five tones at an ISI of one second. There were three conditions. Subjects were delivered an anesthetic gas (N_2O) at either 25% or 35%

dosage or they just received air. Note that N_2O typically reduces the arousal level of subjects. Pang and Fowler averaged tone 1 and tone 2 to 5 across blocks, leading to two averages. The nonspecific (arousal) component should be sensitive to the level of arousal, and hence to N_2O. Because according to Näätänen (1988, 1990, 1992) and Näätänen and Picton (1987) the nonspecific component contributes only to the first trial and not to the subsequent trials, a difference in N100 amplitude due to N_2O should only have been found in the first trial and not in trials 2 to 5. This is exactly what was found, verifying Näätänen's hypothesis.

Verbaten (1990) contended that the nonspecific N100 generator plays a more crucial role in triggering attention than was proposed by Näätänen (1990). Verbaten argued that the refractory period of the auditory nonspecific N100 is not as long as Näätänen claimed it to be (up to one minute and maybe longer). Instead, refractory periods have been found of not more than ten seconds. Verbaten further argued that in visual habituation studies, there is no contribution of the supratemporal component of the N100. Therefore, these studies would provide a better estimation of the contribution of the nonspecific component of the N100. Even with long ISIs, decrement of the vertex N100 was found with repetition of identical visual stimuli (Kenemans et al., 1988; Verbaten, Roelofs, Sjouw, & Slangen, 1986a), ruling out refractoriness of the nonspecific component as an explanation of the decrement of N100. In the study of Kenemans et al. (1989), besides decrement of the visual vertex N100, recovery of the visual vertex N100 was found with ISIs of less than ten seconds. This suggests that the nonspecific component was not in a refractory state. Recovery would not have been found when the generators of the visual nonspecific component were refractory. These results let Verbaten (1990) to conclude that the nonspecific generator contributes to response decrement as well as to the recovery of the visual N100. However, it is still premature to consider the decrement of the visual N100 to be a "genuine" habituation effect because Verbaten and colleagues never measured dishabituation.

In addition to refractoriness, reduced time uncertainty can account for the decrement of the auditory N100 (Näätänen, 1992; Näätänen & Picton, 1987). It is more difficult to predict the onset of the stimulus as ISI increases (e.g., Näätänen, Muranen, & Merisalo, 1974). Thus, in STA paradigms, time uncertainty is large for the first stimulus of a stimulus block because of the long interblock interval relative to the ISI. Time uncertainty is significantly reduced in the ensuing trials. Time uncertainty may thus explain the very fast decrement of the N100 in STA studies, which often reaches an asymptotic level within 2 trials. In the studies of Öhman and co-workers (Maclean et al., 1975; Öhman et al., 1972; Öhman & Lader, 1972), however, it is striking that the decrement of auditory N1-P2 amplitude is more gradual and more persistent than in other STA experiments. How can this difference in the rate of decrement be explained? The Öhman et al. experiments differed from other STA studies with respect to one aspect. Contrary to the customary procedure, a red light heralded the start of each stimulus block. The interval between the light and the first stimulus of a block

corresponded to the ISI between the habituation stimuli, reducing the time uncertainty of the first stimulus. The subject could well predict the first stimulus presentation in a block. Because the decrement of the N100 in STA studies has been mainly found from trial 1 to 2, this initial decrement was reduced in the Öhman studies, resulting in a less steep decrement over the first few trials. An alternative explanation for the missing "first stimulus effect" in the Öhman studies is that the introduction of the visual warning stimulus before the first auditory stimulus may have caused cross-modal refractory effects between those stimuli (Näätänen & Picton, 1987).

A more direct test of the role of time uncertainty in the decrement of the auditory N100 came from Bourbon et al. (1987). In their experiment the initiation of an auditory stimulus block was controlled by either a computer that automatically initiated the blocks, or by the subject itself by pressing a button. Time uncertainty in the automated-initiated stimulus block condition was higher than in the self-initiated stimulus block condition. N100 amplitude to the first stimulus in a block was smaller in the self-initiated condition compared to the automated condition. Thus, the N100 was reduced on the first trial as function of decreased time uncertainty.

To summarize, the decrement of the auditory N100 amplitude may be ascribed to refractoriness of the N100 generators rather than to the reduced novelty of the stimulus induced by repetition of identical stimuli. One argument in favor of this position is that the morphology of the decrement of the N100 – especially with a short ISI – resembles the morphology of the decrement of a response system that is in a refractory state. A second argument is that there is no unequivocal evidence for recovery and dishabituation of N100 amplitude to a qualitative different stimulus. According to Näätänen and Picton (1987), the N100 is large on the first trial because of a large time uncertainty. The N100 decreases with repeated stimulation because of refractoriness of the neural generators of the N100 and reduced time uncertainty. Arguments against the refractoriness hypothesis came from studies with long ISIs and visual stimulus studies. Decrement of the auditory and visual N100 was found with very long (SCR-OR) ISIs. One could argue that the refractory period of the N100 is very long. This argument, however, leads toward circular reasoning. To visual stimuli (e.g., Kenemans et al., 1989) the vertex N100 has been demonstrated to recover. This implies that the nonspecific N100 generator process plays a more crucial role in attention switching than is believed by Näätänen and Picton (1987).

3.3 Mismatch negativity

Näätänen and co-workers carried out a number of studies on the auditory mismatch negativity (MMN). As the name indicates, the MMN is a deviance brain wave. It is evoked by an occasional tone presented among a sequence of identical (standard) tones, even when subjects are not required to discriminate the event categories. The MMN is acquired by subtracting the ERP to the standard stimulus from that to the corresponding deviant stimulus. MMN appears as a negative wave that commences at

about 100 ms from stimulus onset and lasts until about 250 ms after stimulus onset and is sometimes followed by a P3a (Näätänen, 1992). The MMN is composed of two components (Giard, Perrin, Pernier, & Bouchet, 1990; Näätänen & Michie, 1979): a sensory specific one, generated in the auditory cortices and a frontal one. These cerebral generators have been substantiated by source modeling of the magnetoencephalographic (MEG) counterpart of the MMN, by fMRI, positron emission tomography (PET) studies, and intracranial recordings (see for a review Escera, Alho, Schröger, & Winkler, 2000). Stimulus presentation per se is not sufficient for the MMN-generator mechanism because it only reacts to a difference between two consecutive stimuli (Cowan, Winkler, Teder, & Näätänen, 1993; Näätänen et al., 1989). Therefore, in contrast to the N100, no MMN is evoked by the presentation of the first trial in a stimulus sequence. It is assumed that the MMN is generated by a process that registers stimulus deviance (Näätänen, 1992). Näätänen (1990) asserted that the response to the deviance can be characterized as a second order response because the deviance detector must associate two consecutive responses, one for each stimulus. The MMN is generated by the process that encodes the deviance. In this manner, the characteristics of the standard are encoded in a neural trace or representation. MMN reflects the comparison of the current input with the neural trace of prior stimulation.

It is beyond the scope of this thesis to extensively review the antecedents and characteristics of MMN. Instead, some important aspects of the MMN will be enumerated. The MMN is elicited by several types of stimulus changes including changes in pitch, intensity, stimulus duration, sound location, phonetic aspects of vowels, and partial stimulus omission (Näätänen, 1992). ISI has a tremendous influence on the MMN. A long ISI has a limit in eliciting MMN, indicating that the neuronal representation of the standard stimulus decays very fast. Mäntysalo and Näätänen (1987) found that ISIs of 1 and 2 s still elicit MMN, but not ISIs of 4 or 8 s. Eliciting MMN with longer ISIs (up to 10 s) is possible, however, by using a larger stimulus deviation and longer stimulus duration (Böttcher-Gandor & Ullsperger, 1992).

Several findings suggest that the MMN is generated by an *automatic* (preconscious) deviancy detection mechanism. First, predictability does not seem to influence MMN as demonstrated by Scherg, Vasjar, and Picton (1989). They conducted an experiment in which deviant stimuli always occurred after four standards. In the other condition, deviants occurred completely random. Predictability was found to have no significant effect on the MMN. Second, the MMN is not affected by stimulus significance. Näätänen, Simpson, and Loveless (1982) studied stimulus significance by presenting two different deviants of which one was the target. Target deviants elicited a MMN that was similar to the MMN to nontarget deviants. Third, the MMN can be eliminated by masking. A masking stimulus following a test stimulus at a short interval may erase or deteriorate the memory of the test stimulus (Näätänen, 1992). Winkler, Reinkainen, and Näätänen (1993) demonstrated that a deviant stimulus had the properties of a masking stimulus when the interval between standard and deviant was very short

(±150 ms). At these intervals MMN was eliminated. These outcomes confirm the hypothesis that the MMN depends on a memory trace. Fourth, Näätänen (1992) demonstrated the preconscious nature of the MMN by conducting an experiment in which the deviant stimulus was very hard to discriminate from the standard stimulus. Subjects had to indicate whether they thought a stimulus was a deviant or not. Undetected deviants elicited a MMN that was about the same magnitude as the MMN for correct detections, suggesting the existence of a subliminal MMN.

In short, the MMN is elicited by preattentive monitoring of a change in an unattended stimulus sequence (Näätänen, 1988). In this way, the process generating the MMN resembles the model-comparator process in Sokolov's theory. As the OR in the model-comparator theory, MMN is evoked by any stimulus deviance. Furthermore, both the model-comparator theory and the attentional-trace theory of the MMN agree on the fact that respectively, the autonomic nervous system (ANS) OR and the MMN are elicited as a result of a mismatch between the incoming stimulus and an internally held model of previous stimulation. However, MMN differs from the classical OR in several respects. First, the ANS-OR is elicited by the first trial(s), whereas the MMN is only elicited to a stimulus change. Second, the MMN trace is much more short-lived than the ANS-OR. That is, the rates of decay of the memory trace differ, from several seconds for the MMN to minutes for the ANS components of the OR. Third, while the ANS-OR shows rapid habituation over identical stimuli, the MMN hardly declines over repeated deviants (Paavilainen et al., 1987). Fourth, the OR theory incorporates modality-nonspecific effects, while the model for the MMN is probably auditory specific. However, this auditory specificity is disputed in the literature. According to Näätänen (1992), visual or somesthetic phenomena analogous to the auditory MMN have not been unequivocally demonstrated. As an example, Nyman et al. (1990) found a MMN in response to auditory deviant stimuli but not to visual deviant stimuli. In addition, Alho, Woods, Algazi, and Näätänen (1992) found only a visual MMN in response to a salient visual deviant. Alho et al. (1992) conjectured that the difference threshold for a visual analogue of the MMN might be considerably higher than for the auditory modality. Contrary to these findings, Kenemans et al. (1989) ascertained the existence of a visual mismatch wave that was not affected by stimulus relevance and task load, and did not decrease across the deviants. Deviant visual stimuli elicited a large deflection from positive to negative with a latency of 300 ms, the P2-N2. According to Kenemans (1990), as MMN, P2-N2 reflects an automatic mismatch processes. Tales, Newton, Troscianko, and Butler (1999) also found a negativity to unattended visual deviants. Kenemans, Grent-'t Jong, and Verbaten (in press) questioned whether the negativity evoked by visual deviants really depends on a memory trace of the standard. As in the study of Tales et al. (1999) the mismatch wave was elicited by the deviant stimulus. However, the same mismatch wave was also found to lonely deviants without the intervening standards. Apparently, this visual mismatch negativity does not depend on a memory trace. Rather, the negativity is elicited by stimuli with a relatively long

interstimulus interval. In the somatosensory modality, a negative wave was found to unattended deviant stimuli which was interpreted as a somatosensory analogue of the auditory MMN (Kekoni et al., 1997). In contrast to the study of Kenemans et al. (in press), lonely deviants did not elicit a visual deviance wave. Shinozaki et al. (1998) also found a (frontal) MMN-like negativity in response to ignored somatosensory deviants. As the auditory MMN, the amplitude of the somatosensory MMN decreased with a prolonged ISI, suggesting that the somatosensory memory trace decays in a similar manner as the auditory memory trace (Shinozaki et al., 1998). Even in the olfactory modality ignored deviant odors elicit a negative deflection between 500–600 ms with a parietal dominance (Krauel et al., 1999).

The question remains how we can relate the MMN to the OR. According to Sokolov (1960), an OR is elicited when there exists no neural model of the stimulus. A large OR is evoked to the very first stimulus presentation because at that time there is no model of the incoming stimulus. Näätänen and Gaillard (1983) suggested that in the elicitation of the OR to the first trial no comparison mechanism is involved. This hypothesis is corroborated by the finding that the MMN is not elicited by the first trial. The OR evoked by the very first trials in a sequence is called the initial OR by Näätänen and Gaillard (1983). The central component of the initial OR is reflected by a large N100 on the first trial(s). The OR to a change in stimulation is called the change OR and would be indexed by the MMN. The classical OR theory, which is based on nonspecific autonomic measures, makes no distinction between an OR to the first stimulus and to a change stimulus occurring in a sequence of identical stimuli. According to Sokolov (1963), in both cases the same mismatch mechanism is activated because an appropriate neural model is not activated. However, studies on the N100 and the MMN suggest that the change OR involves different cerebral mechanisms than the initial OR. A second issue concerning the relationship between the MMN and the OR is whether the process that generates the MMN serves as a precursor to orienting or whether it is an integral part of the OR (Michie, Siddle, & Coltheart, 1990). It is generally acknowledged that the process that generates the MMN can be considered as a mechanism that stands at the basis of the initiation of the OR. However, the processes underlying the MMN do not in themselves produce conscious perception (Näätänen, 1990). The MMN rather reflects a call from the preattentive mechanisms for central processing capacity (Näätänen, 1988). Thus, the process reflected by the MMN can *initiate* redirecting of focused attention to infrequent stimulus changes (Escera et al., 2000). This brings us to the question whether the OR represents a call initiating processing in a central-channel with limited capacity as originally claimed by Öhman (1979) or whether the OR is the processing itself in a limited-capacity processing mechanism, that is, the result when the call has been successful (Posner, 1975). According to the latter interpretation, an OR is evoked only when stimuli are consciously perceived and is an indication of an actual attention switch. Lyytinen, Blomberg, and Näätänen (1992) argued that it is more likely that an OR is elicited by a stimulus that is

processed in the central channel. Therefore, these authors investigated the question whether the MMN is accompanied by ANS-ORs. It was found that the MMN was evoked independently of ANS-ORs (heart rate and SCR). These results imply that the generators underlying the MMN are automatic and operate without participation of attention and conscious perception and do not necessarily evoke an OR. Only when the MMN is followed by a P3a, attention is actually switched. The P3a component is regarded as a reflection of attention switching itself (Escera et al., 2000).

To summarize, stimulus change, whether or not attended to, evokes a pre-attentative mismatch process that is reflected by the MMN in the auditory modality. In this respect the MMN may be discerned from the N100. The (nonspecific) generators of the N100 primarily respond the very first stimuli in a sequence. Stated differently, the generators of the N100 respond to the initial novelty of a stimulus. Conversely, the MMN is not evoked by stimulus presentation per se but originates from a generator process that is triggered only when incoming stimulation differs from previous stimulation. In addition, although, it was initially thought that the MMN was specific for the auditory modality, some experimental findings suggest that a MMN-like deviance wave can be evoked in several modalities. Finally, the generator process of the MMN does not necessarily lead to orienting but is a prerequisite for an OR.

3.4 P3

The P3 component has repeatedly been associated with the OR. It is a broad positive component, peaking at about 300–600 ms after stimulus onset. Polich and Kok (1995, p. 107) considered the P3 "as a manifestation of CNS activity involved with the processing of new information when attention is engaged to update memory representations."

The P3 can be elicited under a number of antecedent conditions. First, the P3 can be generated in an oddball paradigm when a task is assigned to one category of events (e.g., count the infrequent events) (Donchin, Spencer, & Dien 1997). An oddball task consists of a sequence of events that can be divided in two categories by means of a classification rule (e.g., tones of different pitch). One category is the target, that is, the stimulus to which to the subject has to respond. Targets can be either rare or frequent. Events in the rare category will elicit a P3 regardless whether the eliciting stimulus is the target or not (Duncan-Johnson & Donchin, 1977). Second, the P3 can be elicited in a single-stimulus paradigm. So there is no need, to have two separate categories of events to elicit a P3. Polich, Eischen, and Collins (1994) and Cass and Polich (1997) reported P3 elicitation in a single auditory stimulus paradigm (in which the standard tones were replaced with silence) that was similar to the P3 in an oddball design. Third, a P3 can be elicited in an active discrimination task to an infrequent nontarget stimulus (i.e., a stimulus that is rare but not stimulus-relevant) that is presented in addition to the target and the standard (e.g., Courchesne, Hillyard, & Galambos, 1975). Fourth, the deviant stimulus can elicit a P3 in a two stimulus paradigm in which no intentional discrimination response is demanded (e.g., Squires, Squires, & Hillyard, 1975).

P3 amplitude is interpreted as a manifestation of attention allocation and context updating (Donchin 1981; Donchin & Coles, 1988; Spencer, Dien, & Donchin, 2001). P3 amplitude is under influence of the subjective probability and task relevance of the eliciting events in a multiplicative fashion (Donchin & Coles, 1988). Subjective probability can be divided into a priori probability and sequential expectancies (Johnson, 1986). It is generally acknowledged that there exists an inverse relationship between stimulus probability and P3 amplitude (e.g., Duncan-Johnson & Donchin, 1977). Sequential expectancies are developed on basis of sequential dependencies among stimuli in a sequence (Johnson, 1986). Subjects expect continuation of events when they are confronted with repeated events. Elicitation of the P3 depends on the specific sequence of preceding stimuli. With respect to task relevance (as it is called in Donchin's model), Johnson (1986) asserted that stimulus meaning is a function of task complexity, stimulus complexity, and stimulus value, all three influencing P3 amplitude independently. P3 amplitude increases monotonically with task complexity (Johnson, 1986). Larger P3 amplitudes are elicited by stimuli that are more complex (e.g., Verbaten, 1983). When stimuli acquire stimulus value (e.g., by means of monetary rewards) a larger P3 is evoked compared to stimuli with low-stimulus value (e.g., Begeleiter, Porjesz, Chou, & Aunon, 1983).

The antecedent conditions for elicitation of the P3 resemble those of the OR (Roth, 1983). P3 has therefore been frequently associated with the OR as a central equivalent of the OR. Donchin (1981) asserted that a P3 is evoked as a result of strategic information processing. This information processing is related to evaluating expectancies and affects the way we respond to future stimuli. According to Donchin the process manifested by the P3 affects our schema (representation of the ongoing environment) rather than our actions and reflects memory modification. A P3 is elicited by events that force a change in the ongoing model, or the context, of the environment. A P3 is thus associated with the updating of the schema in the working memory. Context updating resembles the neural (mis)match mechanism of the OR theory of Sokolov (1963). However, a property of P3 that is not shared with the OR is fast habituation. There is no fast habituation of P3 amplitude to the deviant stimuli in oddball paradigms (e.g., Cohen & Polich, 1997). In an oddball paradigm, the deviant stimulus that elicits a P3 has high signal value by means of task instructions. According to Sokolov (1960) stimuli with signal value may evoke a localized OR instead of a generalized OR. Rather than being a nonspecific response, the localized OR is said to arise only in the specific analyzer that is being stimulated. From OR theory and experimental data it is known that the localized OR is more resistant to habituate (Turpin, 1983). Therefore, the P3 that is elicited in an active discrimination task could represent an index of the localized OR to actively attended stimuli.

In short, like the MMN, the P3 is elicited by a surprising event. There are some differences with the MMN. First, the MMN is elicited automatically, whereas the P3 is elicited when a particular event has (been given) some relevance. Second, a P3 can be

elicited by single-stimulus presentations, whereas the MMN is elicited only when a change in a stimulus sequence occurs. The first stimulus in a sequence, whether it is the rare, frequent, target, or nontarget stimulus, elicits a P3 that decreases rapidly with repeated stimulation (see section 3.4.2).

In the current section it was mainly discussed that a P3 can be elicited in situations when stimulus presentations are actively attended to. The next section discusses that an unattended stimulus deviance may evoke different P3 components than an attended stimulus deviance.

3.4.1 Novelty P3, P3a, and P3b

Courchesne (1978) suggested that a distinction must be made between processes indexed by a fronto-central (Novelty) P3 and a parietal P3, based on his experiments with novel stimuli. Evidence for the fronto-central novelty-related P3 came from three-stimulus paradigms that differ from the two-stimulus oddball paradigm in the fact that besides the standard and the target an infrequent nontarget is presented. In an experiment of Courchesne et al. (1975), novel task-irrelevant stimuli (a quasi-random color pattern) were distributed between standards and targets. Unexpected novels evoked a P3 that had a fronto-central distribution. Targets evoked a P3 with a parietal maximum. This so-called Novelty P3 showed fast decrement within three trials (a decrease of 60.1% compared to the first novel). When the novel stimulus was first repeatedly presented and subsequently used as a novel in a stimulus control condition, the P3 at Fz was greatly reduced with respect to the condition with unexpected novels. In the stimulus control condition, the novel stimulus elicited a P3 with a parietal distribution. Thus, decrement of the frontal P3 was observed when the novel stimulus became familiar in content and predictable in time. Similar results were reported by Knight (1984) with auditory stimuli. The P3 evoked by targets had a parietal distribution whereas the P3 to novels had a frontal distribution. No decrement of P3 amplitude to the targets was found, whereas P3 amplitude to novels diminished by 27% from the first to the fifth stimulus. Also in this condition, the scalp distribution of the Novelty P3 shifted slightly from the frontal to the parietal leads. These studies indicate that besides a P3 that is governed by task relevance and subjective probability, a different (fronto-central) P3 is evoked to irrelevant novel stimuli. Courchesne et al. (1975) proposed that the fronto-central P3 and the parietal P3 differ in their functional significance. He contended that the fronto-central P3 may be a sign of the cognitive component of the OR. Courchesne (1978) found a fronto-central distribution of P3 to the first novel stimulus. Whereas P3 amplitude to the target remained unchanged, P3 amplitude to the novels decreased at Fz and increased at Pz. Thus, during the experiment the P3 to novels changed from a fronto-central to a parietal distribution. The difference in scalp distribution may represent differences in the facility with which events may be categorized. Initially, novels were not readily categorized and elicited frontal P3 waves. Due to the build-up of categorization rules applied to the novels, the

frontal P3 distribution shifts to a parietal distribution. Courchesne (1978) concluded that frontal P3 waves would occur whenever new concepts are required and that parietal P3 waves would occur whenever existent concepts are appropriate. In other words, the Novelty P3 is elicited before stimuli are recognized as belonging to a particular category. When categorized, novel stimuli elicit a parietal P3. Simons, Graham, Miles, and Balaban (1998) contended that the process reflected by the frontally distributed P3 might be associated with a generalized OR, whereas the parietal distributed P3 in oddball paradigms might be associated with a localized OR.

In short, it is argued that the Novelty P3 is elicited because of the relative uncodability of the novel stimuli. The necessity of uncodability was disputed by Polich and colleagues. Even simple auditory and visual nontarget deviants can evoke a frontocentral P3 (Comerchero & Polich, 1999; Katayama & Polich, 1998). Katayama and Polich (1998) argued that the stimulus context (i.e., the relative perceptual distinctiveness among stimuli) in which the eliciting events occur, determines whether nontarget deviants evoke a frontal or parietal P3. Polich and colleagues conducted experiments in which the difference between the target and the standard and between the standard and the infrequent nontarget were varied orthogonally. The nontarget evoked an anterior P3 when it was highly deviant in comparison to the target and the standard stimulus. This specific stimulus configuration created a stimulus context in which the nontarget deviant engaged focal attention in a manner similar to that for the novel stimuli in the Courchesne (1975) experiments.

In two-stimulus paradigms in which subjects are instructed not to pay attention to the stimulation, ignored infrequent deviant stimuli may also elicit a frontal P3. In a study of Squires, Squires, and Hillyard (1975), using auditory stimuli, subjects had either to count the deviant stimulus or to ignore it in separate conditions. The probability of the target stimulus was either 0.1, 0.5 or 0.9. In the count condition, the infrequent stimulus, whether or not it was the target stimulus, elicited a parietal distributed P3, called the P3b by Squires et al. (1975). In the ignore condition, infrequent deviants elicited a centro-frontally distributed P3 (P3a). Squires et al. (1975) concluded that the P3a wave reflects any mismatch to an ongoing stimulus train. In later studies on the MMN, it was repeatedly found that MMN is often followed by the P3a (Schröger, 1997). It is assumed that P3a reflects a conscious detection of stimulus deviancy (Schröger, 1997).

Although, in ERP literature the terms P3a and Novelty P3 are frequently used interchangeably, it has been questioned whether the P3a and the Novelty P3 are the same component. Simons, Graham, Miles, and Chen (2001) replicated the experiments of Squires et al. (1975) and Courchesne et al. (1975) to elicit the P3a and the Novelty P3, respectively, and conducted factor analyses on the data sets containing the two components. On basis of their results Simons et al. (2001) argued that the P3a and the Novelty P3 are indistinguishable. Spencer, Dien, and Donchin (2001) came to a different conclusion. They tried to delineate the P3a, the P3b, and the Novelty P3 using

spatiotemporal analysis. These components were recorded in each subject as they all performed a passive oddball task, a "classic" (attended) oddball task, and a novelty oddball task. Their data are consistent with the idea that the P3b and the Novelty P3 are distinct components of the ERP. Furthermore, they hypothesized that the P3a is the result of the summation of a small Novelty P3 with a small P3b. They concluded that there is a distinct Novelty P3, not to be confused with the P3a.

3.4.2 Habituation of the P3 in repetition-change paradigms

As noted in section 3.4, a P3 with a posterior preponderance is evoked in response to the first presentations of a stimulus sequence. In STA studies, fast decrement of P3 amplitude has been found in several modalities (*auditory*: Megela & Tyler, 1979; Ritter et al., 1968, *visual*: Bruin et al., 2000; Megela & Tyler, 1979; *somatosensory*: Kekoni et al., 1997). The expectation of the first stimulus in a sequence has a large influence on the occurrence of the P3. In fact, only when a sequence begins in an unpredictable manner, the first stimulus elicits a P3 (in the auditory modality: Bourbon et al., 1987; Ritter et al., 1968).

Auditory P3 amplitude also shows decrement in response to repeated presentation of identical stimuli with long ISIs in LTA studies (Hirano et al., 1996; Lutzenberger, Shandry, & Birnbaumer, 1979; Roth, Blowers, & Kopell, 1980; Schandry & Hoefling, 1979). In a study of Schandry and Hoefling (1979) the rate of decrement of P3 amplitude was faster than for N100 amplitude (which did not decrease significantly).

In single trial studies using OPTA, repeated presentation of visual stimuli resulted in a decrement of P3 amplitude within a few trials (Kenemans et al., 1989; Verbaten et al., 1986a; Woestenburg et al., 1983). Verbaten et al. (1986a) found that the decrement of the vertex visual N100 was faster than the decrement of the P3.

In a LTA study of Becker and Shapiro (1980), the effect of attention to an auditory stimulus on the N100, the P3, and SCR was investigated. P3 amplitude declined across blocks of 10 trials. P3 amplitude was larger in the attend condition than in the unattend condition. The rate of decrement of P3 was the same for both conditions. Neither the amplitude of the N100 and SCR nor their response decrement were affected by attention. In a single-trial ERP study of Kenemans et al. (1988) the effects of stimulus relevance on the decrement of visual single-trial ERPs and SCR were investigated. In the stimulus-relevant condition, the first stimulus presentations elicited a large P3 amplitude. In the stimulus-irrelevant condition, the first stimulus presentations did not elicit such large P3 amplitudes as in the stimulus-relevant condition. P3 amplitude in the stimulus-relevant condition rapidly decreased to the level of P3 amplitude in the stimulus-irrelevant condition, whereas P3 amplitude in the stimulus-irrelevant condition did not show response decrement. The P3 declined more slowly than N100 and SCR. Kenemans et al. (1989) found no effects of stimulus relevance on the visual P3 and its response decrement.

Recovery of P3 amplitude to a deviant stimulus has been observed (e.g., Kenemans

et al., 1989). In some studies, recovery of the P3 was found while the N100 did not show recovery (Megela & Tyler, 1979; Ritter et al., 1968). Megela and Tyler demonstrated that P3 amplitude showed recovery to both an intensity increase and decrease, whereas N100 amplitude recovered only to an intensity increase. The model-comparator theory advances that recovery is to be expected irrespective of the intensity of the change stimulus. The results of Megela and Tyler suggest that the P3 fulfills this prediction better than the N100. There are hardly any studies that investigate dishabituation of the P3. Megela and Tyler (1979) showed that P3 dishabituated to the habituation stimulus that was presented subsequently to the deviant.

In summary, the posterior P3 that is elicited by the first stimulus presentation in habituation experiments shows important properties of the OR namely, response decrement, recovery, and dishabituation. There is however, disagreement about the rate of decrement of the P3. Whereas some studies found decrement of the P3 that was as fast as SCR or the N100, others found a significant slower decrement than that of the N100 (e.g., Verbaten et al., 1986a). Verbaten et al. concluded on basis of their results that the N100 is involved in a more crude type of stimulus processing than the P3.

3.5 A model of involuntary attention shifts

Studies on deviance-related ERPs such as MMN, Novelty P3, P3a, and P3b contributed to a better understanding of the brain mechanisms involved in passive elicitation of an attention switch. Building on experimental data on the detection of auditory deviants, Schröger (1997) presented a preattentive activation model explaining conscious perception of infrequent deviant sounds in a series of frequent standard sounds.

The model holds that conscious deviance detection is based on the output of an obligatorily operating deviance detection system that acts independently from explicit intention to detect deviants and from attention. The preattentive deviance detection mechanism scans for irregularities in the acoustic input by comparing input with a neural model of acoustic representations. The output may be utilized by attentive processes, resulting in an involuntary attention shift. The model poses two representations of acoustic information. Features of the acoustic input are extracted and encoded into a short-lived (100–200 ms) representation R. Invariances in the recent stimulation are detected and encoded into a more long lived (10 s) representation R' which is probably part of the long auditory store. Contents of R' may be simple features as well as information containing anticipatory power, that is, expectation of future stimulation. The contents of R and R' are constantly compared on a feature specific basis, that is, different features are compared in parallel. This deviant detection mechanism has a preattentive nature. If a discrepancy is detected, the outputs from the feature-specific comparisons converge into an integrated mismatch signal. Whether a mismatch signal results in conscious deviant detection depends on whether the signal exceeds some variable threshold. Only when the variable threshold is exceeded by the mismatch signal, a subsequent stage may be activated resulting in an involuntary attention shift.

In Schrögers model, the P3a is interpreted as a reflection of an attention switch to the stimulus-irrelevant stimulus change. Schröger indicated two ways to influence the probability that the mismatch signal will exceed the variable threshold. First, the threshold depends on the amount of attention paid to the stimulation. The intention to detect deviants consciously reduces the threshold, whereas engagement in some demanding primary task increases the threshold. Attention switches as indexed by P3a may be elicited to irrelevant deviants when the primary task is not demanding, or when the mismatch signal is strong enough to pass the threshold even with highly demanding primary tasks. Implicitly, Schröger considered P3a and Novelty P3 as an index of the same phenomenon. Both reflect involuntary attention switches elicited by a detected mismatch that exceeds some threshold. The second way the threshold is influenced is by the channel separation of stimulus-relevant and stimulus-irrelevant aspects of stimulation. Distractors are more likely to elicit an involuntary attention switch when the target and the distractor are embedded in the same perceptual group or object than when the distractor and the target are embedded in different groups, that is, when the distracting deviant stimulus and the target stimulus occur in separate stimulus streams. Infrequent changes in stimulation are highly surprising when the change occurs in the dimension of the target at which the attention is focused on. To exemplify, large distraction effects were found when a deviation occurred in a stimulus-irrelevant dimension of a stimulus-relevant sound (Schröger, 1996). The subjects in this study were required to discriminate the duration of tones (600 Hz) that were equiprobably long or short, and had to press a button to the long duration stimuli. Infrequently, both long and short tones had a different frequency (650 Hz) that had no stimulus relevance. The (small) frequency deviations elicited a distinct P3a. Schröger (1997) claimed that the distraction effect in the experiment of Schröger (1996) is 3–10 times larger than corresponding effects in distraction paradigms in which distractors occur within the to-be-ignored stimulus sequence.

3.6 ERP studies reveal qualitatively different ORs

From the review of the ERP indices of orienting it has become apparent that different ERP components are differently affected by OR manipulations. Verbaten (1997) identified three qualitative different ORs on the basis of ANS-OR and ERP-OR studies: initial OR (iOR), change OR (cOR), and signal OR. These studies suggest that different mechanisms are involved in the elicitation of these different ORs.

3.6.1 Initial OR/change OR

O'Gorman (1979) proposed to make a distinction between the iOR and the cOR. He suggested that different processes underlie the iOR and the cOR. According to Näätänen and Gaillard (1983), the iOR is evoked as a response to the first stimulus in a sequence, as reflected by a large N100. In contrast to the N100, the MMN is not evoked by the very first stimulus, but is evoked only as a consequence of stimulus

change. Therefore, the MMN is regarded to reflect the cOR (Näätänen & Gaillard, 1983). Because of these different antecedent conditions of both ERPs, it is suggested that different brain mechanisms are involved in the iOR and the cOR. Verbaten (1997) proposed an adjustment of Sokolov's model in which the iOR and cOR are distinguished. Verbaten introduced an "outside channel detector" that can ascertain whether the physical properties of a stimulus fall within or outside the boundaries of the channel. In his model "channel" is defined as a physical property of the stimulus on which an attentional filter is focused. Verbaten assumed that two subsequent processes take place. First, the outside channel detector detects whether the stimulus falls outside the selected channel. Second, a within channel detector is able to detect deviancies within the selected channel. When the presented stimulus (change) falls outside the selected channel, for example, the first stimulus of a habituation series, an iOR will be evoked. When the stimulus change falls inside the selected channel a cOR will be the response. The dissociation between the iOR and cOR is corroborated by the finding that intermodality stimulus changes (outside channel) evoke recovery of the N100 (Fruhstorfer, 1971) and SCR-OR (Furedy, 1968), but no MMN (Näätänen, 1985), whereas with small intramodality (within channel) stimulus changes a MMN is evoked, but no SCR and N100 (Näätänen, 1992). Intermodality stimulus changes are more salient than intramodality stimulus changes and fall outside the range of the selected channel, while small intramodality changes fall inside the selected channel. The first novel stimulus will elicit an iOR because of the absence of an attentional filter.

Verbaten elaborated on the neuronal mechanisms of the model-comparator theory by introducing the role of the thalamus and the reticular nucleus of the thalamus. The reticular nucleus overlaps the specific nuclei of the thalamus and has an inhibitory effect on these sensory relay nuclei. Thus, the transmission of information to the neocortex can be inhibited by the inhibition of the specific nuclei by the reticular nucleus. The reticular nucleus can be inhibited by the MRF resulting in a disinhibition of the specific nuclei in the thalamus. This opens all gates to the cortex, leading to diffuse cortical arousal (Brunia, 1993). An *outside-channel* stimulus causes the MRF to inhibit the reticular nucleus, which enables transmitting of information to the frontal cortex (FC) (Verbaten, 1997). Verbaten stressed that shifts of attention to another channel are most likely located in the specific interaction between the MRF, the reticular nucleus, and FC. With *within-channel* (intramodality) stimulus changes, eliciting a MMN, only the infrequent deviant stimulus is transmitted to the "central processor" via the mismatch route. Within-channel stimulus changes do not activate the MRF. Studies investigating the neural sources of MMN did not find any evidence for the involvement of the MRF in the elicitation of MMN (Csepe, Karmos, & Molnar, 1987; Escera et al., 2000). Further evidence for the absence of the MRF in the elicitation of the MMN came from Lyytinen et al. (1992). They found that the MMN could be elicited without the SCR-OR (which is evoked by the activation of the MRF).

3.6.2 Signal OR

Sokolov (1963) found that the OR to signal stimuli was stronger and habituated slower than to nonsignal stimuli. The question is, whether the nonsignal OR differs from the signal OR not only quantitatively but also qualitatively. This would support the theory of Öhman (1979) in which signal and nonsignal stimuli evoke ORs via different routes. Qualitative differences could be demonstrated if different brain areas are involved in the evocation of signal and nonsignal ORs. Kenemans et al. (1989) conducted a study in which subjects were presented identical visual stimuli interspersed with an occasional deviant. Single trial ERPs and SCRs were recorded to stimulus-relevant and stimulus-irrelevant stimuli. The SCR-OR was evoked only in response to stimulus-relevant deviants, whereas the evocation of P2-N2 (visual mismatch wave) was independent of stimulus relevance. On basis of these results, Verbaten (1997) concluded that different mechanisms are involved in processing of stimulus-relevant and stimulus-irrelevant stimulus changes, although, there is considerable evidence that stimulus relevance is not a necessary factor for eliciting ORs (Öhman, Hamm, & Hugdahl, 2000). The study of Kenemans et al. (1988) provided additional evidence for the hypothesis that signal stimuli elicit a qualitatively different OR. They studied the effect of stimulus relevance on the habituation of visual single-trial ERPs and SCR. Sixteen identical visual stimuli were presented. Half of the subjects were instructed to pay attention to the stimulus, whereas the others were given a neutral instruction. The nonspecific vertex N100 showed fast habituation and was not influenced by voluntary attention. N100 amplitude at Oz was larger in the stimulus-relevant condition with respect to the stimulus-irrelevant condition. In addition, habituation of the N100 at Oz was delayed by stimulus relevance. These results imply a dissociation between vertex N100 and occipital N100. In other words, stimulus-relevant stimuli are processed qualitatively different from stimulus-irrelevant stimuli because they travel along separate neuronal routes (Verbaten, 1997). In the model of Verbaten (1997), the signal OR is elicited via the match route. When a particular stimulus is given signal value by task instructions (e.g., count the high-pitched tones) an a priori neuronal model of the stimulus is formed. When stimuli are presented, both standard and deviant stimuli fall inside the selected channel. Because of this, the collaterals of the specific sensory pathways to the MRF are inhibited. So, the MRF is not activated by this route and the NRT is not inhibited by the MRF. Because of the influence of the neuronal model of the stimulus on the specific thalamic nuclei, the transmission of the deviant stimulus to the frontal cortex is not inhibited, whereas the transmission of the standard stimulus is inhibited. Only, via cortico-reticular pathways the MRF is activated leading to an ANS-OR.

Chapter 4

Motor aspects of the orienting response

4.1 Introduction

From the preceding review of OR theory and physiological indices of the OR, it can be concluded that much emphasis is put on autonomic and central measures. Yet, orienting to novel stimuli also incorporates motor manifestations. From everyday life experience we know that orienting is accompanied by certain motor activities. When someone is confronted with a sudden unexpected stimulus, the concomitant motor behavior may be very diverse. For example, when a bell is swung in front of a baby, we may witness cessation of ongoing behavior (e.g., stopping thumb sucking), turning the head and eyes to the source of the sound, reaching to the bell and manipulating the bell. So, novel unexpected stimuli may induce various exploratory behaviors, but which of them can be identified with orienting? Berlyne (1960) distinguished between behavior primarily belonging to the OR (turning of the head and eyes), secondary exploratory behavior that he calls locomotor exploration (grasping to the bell), and investigatory responses (manipulating the bell). According to Berlyne the OR ends when the subject changes its location in space and/or manipulates the novel object. Hulstijn (1978) maintained, however, that the distinction between primary orienting movements and secondary locomotor/investigatory responses is not clear-cut. In experimental sessions subjects can be engaged in secondary orienting without showing changes in overt behavior. For example, complex visual stimuli may initially evoke turning of the head and eyes, electrodermal and cardiac responses. The subject may subsequently be engaged in secondary exploration. He may, for example, continue to inspect the stimulus and appreciate the beauty of it or make associations with representations in long term memory. Although the boundary between primary orienting responses and secondary investigatory responses is fuzzy, I will consider the OR to be a relatively short-lived phasic motor response. Sokolov would regard motor behavior to be related to the OR when its function is to help resolving initial uncertainty about the environmental stimulus.

The motor responses during the OR were classified into two functionally different subcomponents by Berlyne (1960) and Lynn (1966). The first concerns changes in the skeletal muscles that direct the sense organs (e.g., cats prick up their ears) in order to maximize incoming information. The second motor component concerns changes in general skeletal musculature consisting of a temporary arrest of ongoing activity and a general increase in muscle tonus. Berlyne and Lynn advanced that the second component has a preparatory function in which muscles are mobilized for action. This division of motor components has caused disagreement about the role of the motor activity during orienting. The dispute concerns two issues. First, it is debated whether there is an increase or a decrease in motor activity during orienting. Second, does orienting have a sensory input enhancing or a motor output enhancing function, or both? As already noted in section 1.1, this discussion is suffering from the lack of data pertaining to the motor manifestations of orienting. Therefore, I will review experimental data that have been collected so far concerning changes in the motor system induced by (unexpected,

novel) stimuli (sections 4.3 and 4.4). Before addressing these issues, the next section will first discuss the techniques to study the changes in the motor system.

4.2 Measurement techniques of the motor component of the OR

The motor system is a complex system that can be divided into a number of subsystems. These include the spinal cord, the brainstem, the cerebellum, the basal ganglia, and different structures of the neocortex such as the supplemental motor cortex, premotor cortex, and motor cortex. When we claim to measure changes in the motor system in this thesis, we particularly mean the changes in the lowest level of the motor system, that is, activity of the motoneurons located in the brain stem and in the spinal cord. The motoneurons are called the final common path because all muscle activity results from neural signals traveling along the motoneurons. The output of the motoneurons is modified via different pathways including pyramidal and extrapyramidal tracts. The algebraic sum of excitatory and inhibitory influences on the motoneuron determines if the firing threshold will be reached.

Motor effects of orienting in humans and animals can be studied in several manners. First, one can monitor overt behavior during orienting, for example, with the aid of a (high-speed) camera (Landis & Hunt, 1939) or video (e.g., Ekman, Friesen, & Simons, 1985). Overt behavior in animals is often recorded by scoring movement cessation, head, and ear movements (e.g., Scourse & Hinde, 1973). Second, one can measure the displacement of certain effectors, for instance, eyelid movements (Bohlin & Graham, 1977). The changes in the motor system may be very subtle and therefore can be difficult to score with the observation of overt behavior. A more sensitive technique to study changes in the activity of the motor system is the recording of electromyographic measures of muscle activity (EMG). Recording of EMG activity by surface electrodes, attached to the skin overlying the relevant muscle, makes changes in the activity of muscles visible, which cannot always be detected without that technique. The presence of EMG activity over a certain muscle reflects the firing of agonist motoneurons in the spinal cord or of neurons from motor nuclei in the brain stem. Firing of motoneurons is the result of an excitatory stimulus causing the membrane potential of the cell to cross its firing threshold. Such excitatory influences may originate from widespread spinal or supraspinal sources, for example, from the motor cortex during voluntary action. With increasing excitatory drive, the motoneurons start discharging in a fixed order according to their size and conduction velocity, the so-called size principle (Cope & Pinter, 1995; Henneman, Somjen, & Carpenter, 1965). When the excitatory drive to the motoneuron pool is very small, such that it will not result in a discharge of any motoneuron, the excitability changes in the motoneurons will not be reflected in the surface EMG. Neither become inhibitory influences on the motoneuron membrane potential visible under such circumstances. However, subthreshold excitatory or inhibitory excitability changes can be discovered by eliciting reflexes across the motoneuron pool (Brunia & Boelhouwer, 1988; Capaday & Stein, 1987; Slot & Sinkjær,

1994). If in a baseline condition, a stimulus of a certain strength is used to evoke a reflex, the amplitude of that reflex reflects the number of cells in the pool that discharge. Under experimental conditions, the excitability of the cells in the pool might be changed, resulting in a different response following the same strength of the reflex evoking stimulus. In this manner reflexes can be used as a tool to assess supraspinal and other excitatory influences upon the neurons in the pool. Because reflex amplitudes also reflect subthreshold excitability changes within the motoneurons that, according to the size principle, are inclined to discharge first, reflexes can be considered a somewhat more sensitive measure compared to the surface EMG activity. In the surface EMG, changes in motoneuron excitability can only be discovered when at least one or more motoneurons display firing behavior. However, when this condition has been met, an almost linear relationship may be expected between changes in EMG and reflex amplitudes (Capaday & Stein, 1987; Slot & Sinkjær, 1994).

In summary, reflexes can be employed to probe the activity of the motor system. To study the motor components of the OR, reflexes can be evoked after the presentation of a stimulus. The comparison of amplitudes of reflexes following a stimulus with those of reflexes without a preceding stimulus gives insight in motoric facilitation or inhibition. When reflexes are studied at different tone-reflex intervals the course of motoric activation can be investigated as well. Reflexes can be evoked at different levels of the motor system in various ways. I will discuss the most commonly used reflexes at the spinal level and brainstem level.

At the lumbo-sacral level of the spinal cord, proprioceptive reflexes can be evoked. The reflex arc at the spinal level is composed of several parts (see Figure 4.1). Muscle spindles lie in parallel to the extrafusal muscle fibers (which can cause a muscle to contract) and are attached to them. A muscle spindle contains small intrafusal fibers that are encircled by annulospiral endings of the Ia afferent fibers. The Ia afferent fibers link primarily monosynaptically to the alpha motoneurons. When a tap is given to the Achilles tendon, the calf muscles are stretched, resulting in a stretch of the intrafusal fibers. This causes the annulospiral endings to discharge. An afferent volley advances via the Ia afferent fibers to the alpha motoneurons. Sufficient depolarization of the alpha motoneurons causes a single discharge that propels via efferent fibers to the calf muscle, resulting in a triphasic action potential with onset latency of 35–45 ms when recorded in the soleus muscle (see Figure 4.2).

Another reflex that can be evoked at the lumbro-sacral level of the spinal cord is the Hoffmann reflex (H reflex). H reflexes that are recorded from the calf muscles are evoked by an electrical stimulus to the tibial nerve in the pit of the knee (Brunia & Boelhouwer, 1988). In contrast to Achilles tendon reflexes (T reflexes), H reflexes are not the result of stimulation of the sense organs but of direct electric stimulation of their afferent fibers. The electric stimulation of the afferent fibers causes the alpha motoneuron to fire. The tibial nerve contains both afferent and efferent fibers. Therefore, electric stimulation travels in the direction of the muscle as well via efferent fibers. The

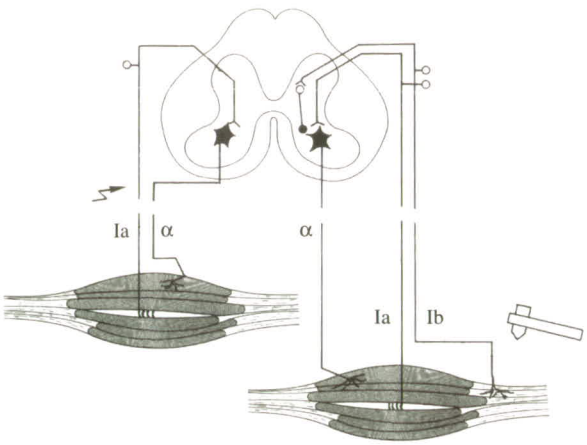

Figure 4.1. The reflex circuit of the Hoffman reflex (left) and the Achilles tendon reflex (right) (Adapted from Brunia & Boelhouwer, 1988).

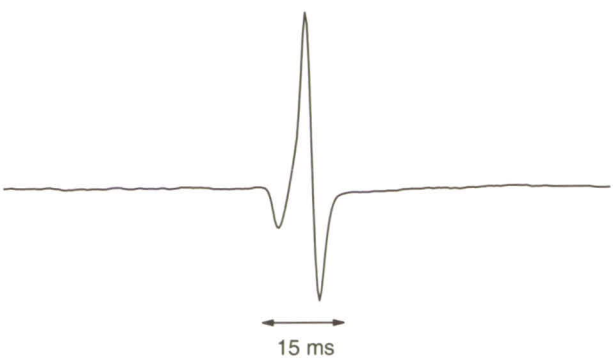

Figure 4.2. Deflection of the Achilles tendon reflex as it is recorded from EMG electrodes.

activation of the efferents results in a muscle contraction called the direct motor response. The retrograde activation of efferents also results in (partial) blocking of the alpha motoneuron output at high stimulus intensities. Further increasing stimulus intensities cause an increased blocking of the alpha motoneuron output, resulting in an inverted U-shaped function of H reflex amplitude with increasing stimulus intensity (Brunia & Boelhouwer, 1988).

At the brainstem level, eyeblink reflexes can be evoked by several kinds of stimuli in different modalities. For example, blink reflexes can be elicited in the auditory modality (loud tones with a short rise time), in the visual modality (intense flashes) and in the somatosensory modality (e.g., electrocutaneous stimulation of the trigeminal nerve). Blink reflexes evoked by electrocutaneous stimulation have two distinct com-

ponents: R1 (onset latency of 8–12 ms) and R2 (onset latency of 25–40 ms). Also, two components can be distinguished in blinks elicited by flashes: R50 (onset latency of 45 ms) and R80 (onset latency of 75 ms). Acoustic blinks have only one component (onset latency of 30–40 ms). Although eyeblink reflexes can be elicited by different modalities, they are considered to be mediated by overlapping neural circuitry (Hackley & Boelhouwer, 1996).

4.3 The motor component of the OR in animals

Overt motor responses in an OR paradigm have not been widely studied in adult humans. However, in several animal studies on the OR, observation of behavior and physiological recordings have been combined. From these studies we can learn about the typical behaviors of different species to novel unexpected stimuli and whether there exists a commonality in OR behavior. I will discuss habituation, recovery, and dishabituation of the behavioral OR and the relationship between the behavioral OR and different physiological measures such as heart rate.

The initial motor response to stimuli shows a remarkable similarity between different species. To loud auditory stimuli the animal shows a whole body startle (e.g., in cats, Sanford et al., 1992; in moles, Aitkin, Horseman, & Bush, 1982; and in rats, Jordan, 1989). Cessation of ongoing activity to auditory stimuli of moderate intensity and to visual stimuli was observed, for example, in rats (Balezina, Markowska, Werka, & Zieliński, 1981; Evans & Hammond, 1983; Walasek, Węsierska, & Zieliński, 1994; Zieliński, 1966), in birds (Gabrielsen, Blix, & Ursin, 1985) and in moles (Aitkin et al., 1982). In several studies, the most common response to novel stimuli was head movements toward the source of the stimulation (e.g., Aitkin et al., 1982; Gabrielsen et al., 1985; Ruusuvirta et al., 1995a; Sanford et al., 1992).

A number of studies investigated habituation of the behavioral OR in animals. Scourse and Hinde (1973) studied overt behavior to different kinds of auditory stimulation in mice when awake or asleep. Auditory stimuli were presented with an interstimulus interval of 30 s. The mice, whether awake or asleep, initially responded to the stimulus with static exploration (rearing and standing sniffing). Static exploration diminished after about 5 minutes of stimulation. The increase in exploratory locomotion to the stimuli following static exploration decreased only over several hours. In other words, primary and secondary exploration were dissociated in the rate of habituation. In rats, habituation of the behavioral orienting response was studied by Nivison, Ursin, and Gjestland (1984). Ninety-six percent of the responses were head and body movements. The number and the amplitude of these movements decreased rapidly within 20 trials. Evans and Hammond (1983) studied the habituation of the OR in rats (the OR was measured as suppression of licking) as a function of stimulus significance. Two stimulus categories (a distress squeal and a mimic squeal) were presented at either 80 dB or 100 dB. Rationale for a real distress squeal is that it is more biologically significant than a simulated artificial squeal. Greater orienting and a slower

decrement were provoked by the loud distress call. When the stimulus was repeated after 1 or 7 days, orienting was considerable larger to the distress squeal than to the mimic squeal.

Apart from response decrement, the OR in response to deviant stimuli has been investigated as well in several studies. Gabrielsen et al. (1985) evoked ORs in incubating Ptarmigan hens in various ways. Stimuli consisted of, for example, sights and sounds of birds, sheep, dogs, and humans. With a telemetry system cardiac and respiratory responses were recorded of the hens in the open field. The hens showed reduced heart rates and respiration, a brief cessation of activity with their heads raised and eyes open. With repeated confrontation of stimuli, inhibition of behavior and head raising as well as cardiac responses decreased and reappeared when a different stimulus (approach of a person) was introduced. Sanford et al. (1993) studied habituation and recovery of the behavioral OR in cats. Habituation stimuli and deviant stimuli were simple auditory sounds presented at an interstimulus interval of 2 s. The behavioral OR decreased rapidly, whereas presentation of the deviant stimulus resulted in recovery of the behavioral OR. Although dishabituation was not tested for, their Figure 4 illustrates that renewed presentation of the original stimulus evoked dishabituation of the behavioral OR. Ruusuvirta et al. (1995a) studied the behavioral OR of cats in a standard auditory oddball situation. The results showed that the head was turned toward the deviant tones, but only in the first few trials. In the following deviant trials, no overt orienting behavior was observed. In a subsequent experiment of Ruusuvirta et al. (1995b), using the same experimental setting as Ruusuvirta et al. (1995a), only a few head movements to the first few standards could be detected. None of the deviant stimuli induced head movements.

In a number of studies it was attempted to disentangle behavior corresponding to startle and orienting. Sanford et al. (1992) presented cats 120 tones of 105 dB with an interstimulus interval of 20 s. Startle was recorded with an accelerometer attached to a wooden platform that was supported by springs on which the cats sat. Data were collapsed into six blocks of 20 trials. The behavioral OR that was composed of head or pinna rotation toward the source of the sound declined rapidly, reaching an asymptotic level at the second block of about 80% decrease compared to the first trial. Of all behavioral responses the head-turning response vanished first. The magnitude of the startle response decreased more slowly over trials to a final level of 40% of the first trial. In addition, the proportion of trials containing a behavioral OR decreased much faster with repeated stimulation than the proportion of trials with startle. The results of Sanford et al. (1992) suggest that behavioral orienting can be elicited by (startling) stimuli along with the startle response. However, a clear dissociation between the two overt behaviors (OR and startle) exists. While the behavioral OR declined relatively fast, the startle response only showed a slow decrement. In an experiment of Aitkin et al. (1982), startle and OR-related behavior of moles could also be qualified as two different motor responses. Motor reactions to pure tones were twofold. When moles

were sitting quietly, auditory stimulation elicited a whole body startle followed by a brief cessation of activity. The second response pattern was observed when the moles were moving. It consisted of a sudden cessation of movement and raising up of the head (sometimes toward the loudspeaker). Grastyán (1959) elegantly demonstrated that startle and the OR are two functionally different responses to stimuli. He recorded electrical rhythmic activity of the hippocampus in cats to various kinds of stimuli. When the stimulus elicited an OR (orienting toward the source of the stimulus) theta rhythms were recorded in the hippocampus. Conversely, hippocampus theta rhythm was desynchronized in response to startle stimuli and to stimuli to which the behavioral OR was habituated.

A related issue is whether the behavior that is scored as a manifestation of the OR is accompanied by heart rate deceleration and whether observed startle behavior is accompanied by heart rate acceleration as suggested by Graham (1979). Heart rate and the behavioral orienting response (head and body movements) in the rat in response to 50 auditory stimuli (white noise bursts of 2 s with a rise and fall time of 1 s and a peak intensity of 85 dB) were studied by Nivison et al. (1984). Three quarters of the animals showed heart rate accelerations and one-quarter heart rate decelerations. Decelerations during the first 25 trials were larger than during the last 25 trials. Accelerations did not decline. The relative frequency and size of acceleration and deceleration did not differ for the presence or absence of the behavioral OR. Thus, the direction of the heart rate change was independent of the occurrence of the behavioral response. In a somewhat different context, Saiers, Richardson, and Campbell (1990) demonstrated in rats that the behavioral component of the OR (head jerk) and cardiac deceleration do covary. It was tested whether arousal induced by electrical shocks prior to the presentation of auditory stimuli would inhibit the OR. The number of shocks was varied (0, 1, 3, 5). Both heart rate deceleration and the number of head jerks were largest with no prior shock and the least with 5 shocks. In the second experiment of Saiers et al., five shocks were delivered. An auditory stimulus was presented following the shocks at a delay of either 0.5, 1, 5, 15 minutes. Both heart rate deceleration and number of head jerks recovered as a function of the delay between the shock and the tones. Contrary to the Nivison et al. (1984) study, these experiments provide evidence that heart rate deceleration is associated with the behavioral OR. Additional support came from Berntson and Boyson (1984) who studied cardiac startle and orienting responses in great apes (infant chimpanzee and gorilla). Tones and vibrotactile stimuli were presented at a variable interstimulus interval of 20–40 s. Behavior was categorized into startle response, nonstartle response, and no observable response. Both vibrotactile and auditory stimuli evoked an initial cardiac acceleration. With repetition of the stimuli, cardiac acceleration was replaced by deceleration. The cardiac response covaried with the categories of the behavioral response. Heart rate showed a short latency acceleration that was associated with startle movements. An initial cardiac acceleration and a late deceleration were observed in trials containing nonstartle movements. Trials showing

no behavioral response were characterized by cardiac deceleration. Also in the study of Gabrielsen et al. (1985), behavior that was scored as belonging to the OR in birds was accompanied by heart rate deceleration.

In summary, animal studies demonstrate that the initial response to unexpected novel stimuli is quite similar for different species. Overt orienting is characterized by head movements and cessation of ongoing activity. The incidence and magnitude of orienting behaviors decline with repetition of identical stimuli, and recover to subsequent deviant stimulation. Loud stimuli induce a whole body startle. Although startle and the OR are functionally different responses, stimuli may subsequently or simultaneously elicit startle responses and orienting responses, when behaviorally measured. Behavior that is accordingly scored as orienting behavior is accompanied by heart rate deceleration, while startle is marked with heart rate acceleration.

4.4 The motor component of the OR in humans

4.4.1 Overt behavior

Overt behavior in adult humans during orienting is seldom investigated (Spinks & Siddle, 1983). One of the reasons is that in an artificial experimental environment subjects often have to sit as still as possible to minimize movement artifacts in the physiological recordings. Nevertheless, exploratory behavior in infants and neonates has been widely studied. Novel stimuli evoke various behaviors, such as reduced activity, suppression of sucking, widening of the eyes, visual fixation, and head turning toward the stimulus (Graham, Anthony, & Zeigler, 1983). Habituation and recovery of the behavioral OR have been demonstrated in infants (e.g., Graham, 1984; Cohen, 1976; Zelazo, Brody, & Chaika, 1984).

In some studies, overt behavior in adults was scored in response to startling stimuli such as gunshots. For example, Landis and Hunt (1939) and more recently Ekman et al. (1985) described the startle reflex in great detail with the aid of high speed photography and video, respectively. The startle pattern consists of an eyeblink, head movement, hunching of the shoulders, flexion of elbows and fingers, and bending of the knees. Of all bodily responses the eyeblink was the most reliable, it was always present. The startle invariably started with a blink and progressed downward across the body. Recently, Turpin, Schaefer, and Boucsein (1999) examined habituation and recovery of head and body movements to auditory stimuli that varied in duration, rise time, and intensity. The stimulus characteristics were chosen to elicit either startle, OR, or defense responses. The magnitude and the incidence of head and body movements increased with increasing intensity and decreasing rise time, and diminished over trials. A qualitative different stimulus at the end of the habituation series, however, failed to cause a reliable increase in head and body movements.

A problem with the behavioral OR is that it is often scored as an all or nothing phenomenon, for example, head or no head turning toward the stimulus source. A

second concern is that different OR behaviors are often compiled into a single score. Roussounis and Gaussen (1987), for example, employed a sophisticated observation scheme. ORs in neonates were scored when one of the following behaviors was detected: head and eyes movements, stilling of the head, eyes, face, arm, leg, or trunk movements, and slowing of breathing. However, no differentiation between different behaviors was made, all were interpreted as manifestations of orienting. These scoring procedures typically result in a relatively imprecise measurement of the behavioral OR, like the number of trials with an OR or the number of subjects displaying an OR. A detailed description of the course of overt behavior over time is not often reported.

Despite the difficulties with the behavioral OR under experimental conditions, as mentioned in the beginning of this section, a particular aspect of orienting behavior has recurrently been studied: the visual orienting response (VOR) that consists of turning the eyes to the source of stimulation (Verbaten, Woestenburg, & Sjouw, 1979). Eye movements can be readily studied under experimental situations. In experiments studying the VOR, it is argued that novel stimuli cause the eyes to fixate on the novel stimulus. With stimulus repetition, fixation time would decrease due to the loss of novelty of the stimulus. Mackworth and Otto (1970) presented children of age 2–7 years a 4 x 4 matrix with white geometric shapes for ten times. On the next twenty trials one single item was colored red instead of white. The image of the matrix that reflected off the pupil was recorded by a motion picture camera at a rate of 5 frames per second. Fixation was determined by recording which part of the matrix was centered in the pupil. The results showed a considerable increase in fixation time to the novel stimulus. The time spent viewing the novel stimulus linearly declined in the subsequent trials. In a study with adult subjects, Furst (1971) presented six color photographs 5 times in a quasi random order. The technique to measure the location of the gaze was the same as in the experiment of Mackworth and Otto (1970). Each picture was broken up into 64 sectors. The number of changes of the gaze from sector to sector was recorded. Within each trial, the mean number of fixations in the second half of the presentation time (3 s) of the picture had decreased compared to the first half. Repeating the same picture resulted in a decrease of the mean number of fixations per trial while the predictability of fixations increased. In other words, the distribution of the number of fixations in each sector and the total time spent fixating in each sector became more stereotyped. This was also true for the order in which objects in the pictures were searched.

Verbaten and co-workers (Verbaten et al., 1979; Verbaten, Woestenburg, & Sjouw, 1980; Verbaten, Woestenburg, Sjouw, & Slangen, 1982) conducted a number of experiments on the habituation of the VOR. Visual stimuli were presented on a monitor and located in the periphery of the visual field. It was supposed that subjects would make a saccadic eye movement to inspect the stimulus. In addition, it was expected that saccadic eye movements (and thereby total fixation time) would show habituation with repeated presentation of identical stimuli because the need to extract information from

the stimulus would have been reduced. Eye movements were recorded by means of the electro-oculography (EOG). The VOR (measured as fixation time per trial) significantly decreased as a result of repeated presentation of identical stimuli (Verbaten et al., 1979; Verbaten et al., 1980; Verbaten et al., 1982). When Verbaten, Kenemans, Sjouw, and Slangen (1986b) recorded fixation time with a corneal reflection technique, no decrement of fixation time was found. What is the reason that two different techniques supposed to measure the VOR led to conflicting results? Verbaten et al. (1986b) maintained that in their experiments, the subjects anticipated the presentation of the stimulus. That is, before each stimulus presentation they looked for longer periods to the location where the stimulus would appear. The EOG technique lead to false estimations of the VOR because of this looking behavior (Verbaten et al., 1986b). They therefore concluded that the habituation effect of the (EOG-) VOR was most probably artifactual. The fact that Verbaten et al. (1986b) did not found habituation of the VOR does not necessarily imply that in the natural environment fixation time does not decline as the novelty of the stimulus decreases. As implicitly indicated by Verbaten et al. (1986), in artificial experimental conditions, looking behavior may be quite different from that in everyday life. At the start of the experiment the adult subject often knows that something is presented (especially when this information is explicitly presented) and that this is done for some reason. In order to be a "good" subject he will continue to monitor the stimuli carefully because to his opinion the stimuli are likely to be important for the purpose of the experiment and because this is probably what the experimenter expects from him. This problem may be avoided by presenting the subject a primary task during which an occasional deviant stimulus is presented. Tales, Newton, Troscianko, and Butler (1999) presented visual standard stimuli interspersed with an occasional target stimulus to which subjects had to respond. Additionally, deviant nontarget stimuli were presented outside the focus of attention in the peripheral field. It was found that the mean EOG during presentation of the nontarget deviants was virtually identical to that during presentation of standards or targets, indicating that subjects (eventually) ignored the nontarget deviants. Nontarget deviants evoked a visual equivalent of the auditory MMN without a P3a, providing additional evidence for the fact that although the brain registered the deviant stimuli, subjects ignored them. In short, when the subjects were engaged in a primary task, task-irrelevant visual stimuli did not evoke a VOR. It is unfortunate that Tales et al. (1999) did not report whether the VOR showed habituation across the nontarget deviant stimuli. It is conceivable that in this experiment irrelevant deviant stimuli elicited a VOR to the first few nontarget deviants. With repetition of the nontarget deviant, a possible VOR would disappear as the presentation of the nontarget deviant looses its novelty. Because data were averaged across 32 deviants, the VOR to the first nontarget deviants was probably lost in the average. It would be particularly interesting to examine whether the first deviants would have evoked a P3a concomitant with the VOR.

4.4.2 Electromyographic studies

Several studies have been conducted on the effect of stimulus presentation on generalized EMG responses or EMG responses of specific muscles. A considerable part of this research area is devoted to startle responses. Startle eliciting stimuli share two common properties. The (auditory) stimulus should be rather intense and have a sudden onset. The EMG motor response to startle eliciting stimuli has a short latency and short duration (Brown et al., 1991; Chokroverty, Walczak, & Hening, 1992; Sachdev, Cheem, & Aniss, 1997; Wilkins, Hallett, & Wess, 1986).

A number of studies used reflexes as a tool to estimate descending influences, induced by auditory stimulus presentation, from supra-spinal structures upon segmental circuits. The amplitude of spinal reflexes is enhanced after auditory stimulus presentation. Enhancement of the reflex amplitude lasts about 250 ms and is maximal at about 100 ms after stimulus onset.[1] This effect was demonstrated with knee jerks (Beale, 1971), H reflexes, and T reflexes (Delwaide & Schepens, 1995; Paillard, 1955; Rossignol & Melvill Jones, 1976; Rudell & Eberle, 1985). Additional evidence for audiogenic influences on the motor system came from the warned reaction time paradigm. In a typical warned reaction time experiment, a warning stimulus (WS) is presented indicating that a response stimulus (RS), to which the subject has to respond, will follow within a few seconds. Motor preparatory processes can be studied by means of eliciting spinal reflexes in the interval between WS and RS. It has repeatedly been demonstrated that an auditory warning stimulus has a facilitatory effect on the amplitude of a subsequently elicited reflex at 100 ms after stimulus onset (Brunia, Scheirs, & Haagh, 1982; Requin, Bonnet, & Semjen, 1977; Scheirs & Brunia, 1982; Scheirs & Brunia, 1985). Brunia and Boelhouwer (1988) hypothesized that a (warning) stimulus provokes a generalized increase in the excitability of motoneuron pools along the neuraxis as part of an alerting process. They implicitly associate this short latency increase in the excitability of motoneurons with the OR, in its function to facilitate motor output: "this suggests that the warning stimulus indeed alerts the whole motor system to be ready for action" (Brunia & Boelhouwer, 1988, p. 60). Audiogenic reflex facilitation might indeed be associated with the OR because it possesses an important property of the OR, namely response decrement with repeated stimuli. The amplitude of spinal reflexes, evoked 100 ms after stimulus onset, decreases with repeated presentation of identical stimuli (Rossignol & Melvill Jones, 1976; Rudell & Eberle, 1985)

At the brainstem level the prepulse modification paradigm can be used to investigate motor effects induced by stimulus presentation. In this paradigm a non-startle eliciting stimulus is followed by a startle eliciting stimulus. The magnitude of the response (eyeblink) to the startle eliciting stimulus is modified by the preceding

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1 When in this thesis it is stated that the reflex amplitude is maximal at 100 ms after stimulus onset, it is meant that the reflex amplitude is maximal when the reflex is evoked at 100 ms after stimulus onset. The moment of maximal facilitation of the motoneurons is somewhat later (±20 ms) because of the time that is needed for the afferent volley to reach the alpha motoneurons.

weak lead stimulus (prepulse). Depending on the interval between the lead and the reflex eliciting stimulus, reflex amplitude can either be facilitated or inhibited by the prepulse. With short intervals, less than 100 ms, the eyeblink is facilitated (Hackley & Boelhouwer, 1997). According to Graham (1975), this facilitation reflects an arousal mechanism with a nonspecific motor response. In addition, facilitation may be due to energy summation of the reflex eliciting stimulus and the prepulse. At intermediate intervals of 30–500 ms between the prepulse and the reflex eliciting stimulus, reflex amplitude is inhibited (e.g., Filion, Dawson, & Schell, 1998). Graham (1975) maintained that this inhibition reflects the protection of the preattentive processing of a stimulus from disruption by startle during the time needed to process the stimulus.

In contrast to the generalized motor responses described above, some responses have been found to be sensitive to the spatial direction of the stimulation. Besides the eyes, as discussed in section 4.4, the head is turned to the source of the novel stimulus. This directional turning of the head in humans was investigated by Matson (1980). He conducted an experiment to investigate the existence of a sonomotor head-turning reflex by recording the activity of left and right sternocleidomastoideus. Note that a right sternocleidomastoideus contraction turns the head to the left, and vice versa (Mayoux-Benhamou, Revel, & Vallee, 1995).

Subjects sat in front of two laterally positioned loudspeakers from which clicks (bursts of white noise with 29.8 ms duration) of 60 dB sounded. The clicks were presented randomly from either the left or right speaker at a rate of 5 per second. Subjects were instructed to listen passively to the stimulation. The stimuli evoked a short-latency activity only in the sternocleidomastoideus contralateral to the stimulation, suggesting a head-turning reflex toward the source of stimulation.

So far, only early motor responses to (auditory) stimuli were discussed. In a few studies, prolonged motor responses during presentation of auditory stimuli of long duration (ranging from 4 s to 45 s), were recorded. In these studies, the effect of auditory stimulus presentations on facial muscle EMG was investigated. Participants listened passively to simple or complex tones of a relatively high intensity (ranging from 75 dB to 109 dB) and made affective ratings about the stimuli. It was found that stimulus presentations produced elevated facial EMG levels of corrugator (Kjellberg, Sköldström, Tesarz, & Dallner, 1994), zygomaticus and corrugator (Dimberg, 1990) and frontalis, corrugator, and orbicularis oculi (Jäncke et al., 1996) (see Figure 6.1 for locations of these muscles). In the studies of Dimberg (1990) and Kjellberg et al. (1994), activity of the corrugator muscle increased with increasing stimulus intensity. Jäncke et al. (1996) found a positive relationship between activity of both frontalis, corrugator and orbicularis oculi and intensity of environmental noises. Because these studies employed relative high stimulus intensities, there is a possibility that defensive responses were evoked instead of ORs. The affective ratings that participants had to make after each stimulus presentation in the EMG studies also point to elicitation of defensive responses because perceived annoyance increased with increasing stimulus intensity.

To summarize the EMG studies, human studies investigating the motor (EMG) response to stimulus presentation, focused mainly on the startle response. These studies demonstrated that auditory stimuli may cause a generalized short-latency response of which the magnitude increases with stimulus intensity. Short-latency activity in neck muscles (sternocleidomastoideus) was found to be sensitive to the direction of the stimulation as well. A few studies found in several facial muscles prolonged, increased EMG activity to strong auditory stimuli of long duration, however, probably reflecting defensive responses.

4.5 The motor function of the OR

As noted in sections 1.1 and 4.1, in OR literature it has been debated whether the OR affects the perceptual system for more efficient information processing, or whether it enhances response execution. In the tradition of Pavlov, Sokolov (1960, 1963) argued that the OR should be looked upon as a "What-is-it? response", whereas Germana (1968, 1969) argued that the OR is much more a "What-has-to-be-done? response." Sokolov (1963) advanced that the motor effects of the OR presumably subserve an enhancement of perceptual sensitivity. Germana on the other hand maintained that the function of the OR is first of all to facilitate motor processes, and to prepare the organism for action. This contradiction between both hypotheses is discussed in more detail in chapter 5. For now, I will focus on an important implication of Germana's theory. During the OR, muscle tone is believed to be increased in order to get into a state of preparation. Increased muscle activity is a functional response because it facilitates reaction times (Haagh, Spoeltman, Scheirs, & Brunia, 1984; Sanders, 1979; Scheirs & Brunia, 1986; Spijkers, 1990). Is there any evidence for increased muscle activity during an OR? As recapitulated in section 4.4.2, a rapid short-latency increase in motor activity in several muscles is evoked by loud tones with short rise times. This burst of motor activity at high stimulus intensities, however, is considered to be the startle response and not related to the OR. If this early activity would be related to the OR one would expect that a highly novel and surprising stimulus would also induce enhancement of motor activity at lower stimulus intensities. However, this has never been systematically studied. Second, in contrast to the startle response that has a brief output at short latency, the OR is characterized by a relatively prolonged output (Cook & Turpin, 1997). Consequently, if orienting constitutes a preparation to respond, a more prolonged muscle activity than the startle response is to be expected. Studies that incorporated motor effects at longer latencies are scarce. Those studies that did record longer-latency EMG muscle responses, for example, Davis (1948, 1950) suffered from methodological flaws (as enumerated by Van Boxtel & Jessurun, 1993), or did not measure EMG in the relevant muscles such as postural muscles and muscles in the limbs (Dimberg, 1990; Jäncke et al., 1996; Kjellberg et al., 1994). In addition, in the studies of Davis, the occurrence of the long latency muscle activity was less stable than the early motor response. So, the presence of (longer latency) EMG activity during

orienting, subserving motor output processes, has not yet been unequivocally established.

The second issue in the dispute of the motor function of the OR concerns the presumed inhibition of ongoing activity. In animal and infant studies, novel stimuli initially induce, besides stimulus-directed movement of the sense organs, inhibition of ongoing activity at the behavioral level (see section 4.4.1). At the same time it is presumed that muscle tone is increased (Berlyne, 1960; Lynn, 1966). Spinks and Siddle (1983) advanced that the suggested inhibition of behavior seems to conflict with the proposal that the OR results in a general increase in muscle tone. The relevant question in this matter is, however, how inhibition of ongoing activity is realized? Does it consist of passive relaxation of agonist muscles or of active isometric rigidity by concurrent tensing agonist and antagonist muscles? In the latter case inhibition of ongoing activity is accompanied by increased muscular activity. An important consideration with respect to these questions is to which muscles the inhibition applies. It is conceivable that the function of a particular muscle in interaction with the postural position determines the specific response. When a person is standing, relaxation of the postural musculature would be inappropriate. It is possible that some subsystems of the motor system show excitation whereas at the same time other subsystems are inhibited. This division in activation of muscle activity was demonstrated in another research field. In a series of warned reaction time tasks, Obrist and colleagues observed that somatic activities in muscles that were irrelevant for the task at hand, such as the mylohyoideus muscle, were inhibited, accompanied by heart rate deceleration (e.g., Obrist et al., 1974; Obrist, Webb, Sutterer, Hebb, & Howard, 1970). Obrist et al. (1970) hypothesized that inhibition of ongoing activity originates from a central mechanism with the purpose to prevent irrelevant activities to compete with the specific task-relevant motor and sensory activities. Because heart rate deceleration covaried with striate muscle inhibition, Obrist hypothesized the existence a of cardiac-somatic coupling.

The cardiac-somatic coupling hypothesis was challenged by other studies. Inhibition of task-irrelevant motor activity other than EMG activity of the mylohyoideus muscle (e.g., muscles of the shoulders, arms, and legs) during the warning period could not be demonstrated in subsequent studies (Brunia & Vingerhoets, 1980; Haagh & Brunia, 1984, 1985). Muscle activity remained unchanged or increased in the foreperiod, whereas at the same time heart rate decelerated. Brunia (1984) and Van Boxtel, Damen, and Brunia (1996) suggested that anticipatory inhibition of muscle activity may apply only to muscles that are innervated by cranial nerves. Van Boxtel et al. (1996) found that in the warning interval, activity of muscles in the lower part of the face and the masticatory apparatus (orbicularis oculi, zygomaticus, temporalis, masseter, and mylohyoideus) was gradually inhibited in anticipation of the response stimulus. Simultaneously, facilitation of EMG activity was found for corrugator supercilii. Heart rate decelerated consistently, irrespective of the direction of EMG activity in different pericranial (facial) muscles within the same interval, thereby refuting the "strong version" of the cardiac-somatic coupling hypothesis. However, stronger heart

rate deceleration was accompanied by stronger inhibition in the muscles that were inhibited and by less facilitation in the muscles that were facilitated. This finding supports a "weak version" of the cardiac-somatic coupling hypothesis. Discussing the cardiac-somatic coupling hypothesis, Brunia (1984) pointed at a different function for trunk and extremities muscles as compared to pericranial muscles. Some of the pericranial muscles play a role in communication of information. He speculated that inhibition of pericranial muscle activity is a functional response because "by reducing noise selective quieting in this communication system could contribute to better perception and therefore better preparation for a response" (Brunia, 1984, p. 215). Van Boxtel et al. (1996) suggested that inhibition of pericranial muscles in the lower part of the face might increase both directly and indirectly the perceptual (auditory) sensitivity to external stimuli. The direct effect would imply that inhibition of these muscles would increase auditory sensory sensitivity because of reductions of internal auditory noise, produced by involuntary contractions of the muscles in the lower part of the face and the masticatory apparatus. Indirectly, pericranial inhibition would be accompanied by relaxation of middle ear muscles, producing lower auditory thresholds for low-frequency sounds.

4.6 Research questions

From the review of the motor manifestations of orienting we can conclude that there are many blind spots in the knowledge and understanding of the motor aspects of orienting. First of all, to our knowledge, there is virtually no human study in which electromyographic activity was systematically recorded in an OR paradigm. Therefore, the present research aimed at investigating changes in activity of several muscles during the course of the OR in a systematic manner. It was stated earlier that EMG is a useful tool to gain insight in the changes of the motor system because it can detect very subtle motor activity that is sometimes difficult (if not impossible) to uncover with the observation of overt behavior. Alternatively, spinal reflexes (T reflexes) may be evoked during or after the presentation of (novel) stimuli. With this technique, changes in the excitability of the motoneurons may be revealed, resulting in an even more sensitive measurement of changes in motor activity than EMG recordings. In this thesis both techniques were used to study the motor effects of orienting. The main research question was:

> *What are the changes in the motor system, as indexed by EMG and T reflex amplitude, to unexpected novel stimuli?*

Do variables including stimulus novelty, stimulus significance, stimulus intensity, and stimulus repetition influence stimulus-related activity in the motor system? Do motor response patterns correlate with other physiological indexes of the OR such as SCR, heart rate, respiration, and OR-related ERPs? To assess the motor components of the

OR, it was examined whether stimulus-related motor activity satisfied the defining properties of the OR such as response decrement with presentation of identical stimuli, recovery to a stimulus change, and dishabituation to the renewed presentation of the habituation stimulus. Research paradigms were used that have previously yielded reliable autonomic and central indices of the OR.

The main research question was subdivided in two questions pertaining to the function of motor processes during orienting. First, is there evidence for the hypothesis that the OR involves a preparation for action? If the OR prepares the organism for action, a general increase in motor activity is to be expected after presentation of (novel) stimuli. In chapter 5, stimulus-related changes in the motor system were studied by evoking T reflexes after the presentation of auditory stimuli. It was investigated whether audiogenic spinal reflex facilitation can be considered an integral part of the OR, reflecting facilitation of the motor system with the function of facilitating response execution. The aim of the experiments was to examine whether audiospinal facilitation would satisfy the most important characteristics of the OR, including response decrement with repeated presentation of identical stimuli, recovery to a stimulus change, and dishabituation. Additionally, it was tested whether T reflex amplitude was affected by the experimental manipulations in a similar manner as autonomic indices (SCR) and cerebral indices (N100, MMN, P3) of the OR.

Alternatively to the hypothesis that during the OR the motor system is facilitated in order to bring the organism in a preparatory state, motor manifestations of the OR might entail sensory facilitation as suggested by Sokolov (1963). Therefore, the second question relating to the function of motor processes during orienting is whether we can identify stimulus-related changes in motor activity that increase the analyzer sensitivity, which according to Sokolov (1963) is the primary function of the OR (see chapters 6 and 7). A valuable study in this respect is that of Van Boxtel et al. (1996) who studied pericranial muscle activity in a warned reaction time task. On the basis of their results they related certain muscle responses to sensory sensitivity. Specifically, they hypothesized that inhibition of lower facial and masticatory muscle activity increases (auditory) sensitivity. Consequently, if the primary function of the OR would be to increase the sensitivity of the perceptual system, inhibition of pericranial muscle activity during the course of the OR may be predicted. Inhibition of pericranial muscle activity might thus improve the perception and processing of the OR-eliciting stimulus.

Chapter 5

Probing the orienting response with Achilles tendon reflexes

5.1 Abstract

The present study examined changes in the motor system during the orienting response (OR) by evoking Achilles tendon reflexes (T reflexes) after presentation of (novel) auditory stimuli. The first two experiments comprised a repetition-change paradigm in which T reflexes were evoked at 100 ms after tone onset. T reflex amplitude decreased across presentation of identical stimuli. The rate of response decrement was comparable to that of SCR (skin conductance) and N100 that were recorded in Experiment 2. In Experiment 1, T reflex amplitude recovered to a stimulus of higher intensity, but not to a stimulus of lower intensity. Dishabituation was significant after both intensity increase and decrease. In Experiment 2, T reflex amplitude showed recovery to a change in pitch. There was no main effect of dishabituation of T reflex amplitude. In Experiments 3 and 4, T reflexes were evoked in an oddball paradigm at different intervals after tone onset (100, 200, 300 ms in Exp. 3; 200, 300, 400, 500 ms in Exp. 4). A change in pitch that was either attended to or ignored, evoked elevated T reflexes in comparison with the standard immediately preceding the deviant only at intervals of 200 and 300 ms in Experiment 3. In Experiment 4, stimulus deviance had no effect on T reflex amplitude. It is concluded that the audiogenic facilitation of T reflex amplitude is subjected to habituation and is sensitive to stimulus deviancy if the stimulus change involves a high arousal value or a large difference in pitch compared to previous stimuli. The results are discussed in relation to the functional significance of audiogenic reflex facilitation.

5.2 Introduction

The orienting response (OR) can be defined as a complex of behavioral and physiological responses to unexpected, novel, and sudden changes in the stimulus environment (Sokolov, 1963). Behavioral and physiological responses include interruption of ongoing activity, directing the sensory organs to the stimulus, autonomic changes such as heart rate deceleration and an increase in electrodermal activity, and changes in brain activity as indexed by EEG desynchronization and event related brain potentials. There are two perpendicular theories regarding the function of the OR. Sokolov (1963, 1969) claimed that the functional significance of the OR is to increase the analyzer sensitivity, resulting in facilitation of the uptake, transmission, and analysis of environmental information. An illustration of the sensory function of the OR is the orientation of the sense organs toward the source of the stimulation, first, in order to optimize closer perception of the eliciting stimulus and, second, to anticipate probable sources of future stimulation. These motor behaviors are believed to be conducted in order to resolve the question "What is it?." Other authors, however, share the opinion that the primary function of the OR is to facilitate motor processes rather than sensory processes. They presume that the organism is primarily concerned with the question "What has to be done?", and that besides sensory facilitation the OR constitutes a preparation for action (Germana, 1968, 1969; Lynn, 1966; Ruttkay-Nedecky, 1967, 1969). The OR is said to induce cessation of ongoing activity and inhibition of task irrelevant behaviors while

facilitating task-relevant behaviors (Lynn, 1966). According to Germana (1969), increased muscle tone, EEG desynchronization, and cardiovascular responses represent a general preparation to respond. He further noted that the organism is primarily concerned with behavioral requirements, and that enhancement of sensory sensitivity is subordinate to behaviorally efficient adaptation to changes in the environment. Germana conjectured that the neuronal model of the stimulus also includes the characteristics of associated responses. Central to the reasoning that the OR constitutes a preparatory function is the supposed increase in readiness for activity in the skeletal muscles (Lynn, 1966). Berlyne (1960) advanced that skeletal musculature is mobilized for swift execution, indicated by increased muscular activity. Increased muscle tone would cause the motor system to be brought closer to the motor action limit which would result in faster responding. There is indeed some evidence for the proposed functional significance of facilitation of muscle activity. Several studies have found that deliberate tensing of the relevant muscles in anticipation of a response signal facilitates response execution (Haagh, Spoeltman, Scheirs, & Brunia, 1984; Sanders, 1979; Scheirs & Brunia, 1986; Spijkers, 1990). However, apart from the fact which of both positions regarding the function of OR is more plausible, there are surprisingly few studies investigating the changes in the motor system during the OR. Thus, although some authors attribute a motor-preparatory function to the OR, this is not substantiated by convincing experimental evidence (see chapter 4).

In the current study, it is questioned whether there is an instantaneous generalized facilitation of the motor system that is associated with orienting. A technique to demonstrate changes in motor activity is the evocation of reflexes at different levels of the neuraxis. A major advantage of the use of spinal reflexes as a probe over recording surface electromyography (EMG) is its higher sensitivity to reflect changes in the motor system. Even subthreshold excitatory or inhibitory excitability changes can be discovered by eliciting reflexes across the motoneuron pool (Capaday & Stein, 1987; Slot & Sinkjær, 1994). This superior sensitivity of reflexes over EMG was demonstrated in a forewarned reaction time task by Scheirs and Brunia (1985) as movement preparation modulated Achilles tendon reflexes (T reflexes) but not bipolar EMG activity recorded in the soleus muscle.

Auditory stimulus presentation induces a generalized facilitation in motor activity. Spinal reflex amplitudes are enhanced from 50 ms to about 250 ms after stimulus onset (Beale, 1971; Delwaide & Schepens, 1995; Liegeois-Chauvel et al., 1989; Rossignol & Melvill Jones, 1976; Rudell & Eberle, 1985; Scheirs & Brunia, 1982). Reflex facilitation is maximal at about 100 ms after stimulus onset. Brunia and Boelhouwer (1988) advanced that this audiospinal facilitation is part of an alerting process. It might thus be reasoned that the enhancement of reflex amplitude is an OR-mediated effect. If so, reflex facilitation should display the defining characteristics of the OR, including response decrement across repeated presentation of identical stimuli, recovery in response to a deviant stimulus, and dishabituation to the renewed presentation of the original stimulus. There is some evidence that the amplitude of spinal reflexes evoked at 100 ms

after stimulus onset decreases as a function of stimulus repetition. Rossignol and Melvill Jones (1976) evoked ten Hoffman reflexes (H reflexes) at 100 ms after initiation of tones of 110 dB at an interstimulus interval of 15 s. A significant amount of decrement was found. H reflex amplitude on the last (tenth) tone was about half of that on the first tone. Rudell and Eberle studied (1985) found decrement and recovery of the facilitation of H reflexes to tones of 80 dB. Twenty-four tones were presented to either the left or the right ear. The interstimulus interval varied between three and more than several tens of seconds. H reflexes were evoked 100 ms after tone onset. After the stimulus series, one tone was presented to the opposite ear to test recovery. The results showed a response decrement that was much smaller than reported by Rossignol and Melvill Jones (1976), probably because of the greater time uncertainty induced by the irregular ISI. The H reflex did not show recovery when the tone sounded in the opposite ear.

In the experiments in this chapter, T reflexes were evoked after simple auditory stimuli of moderate intensity that were supposed to evoke ORs. In order to determine whether the audiospinal facilitation reflects motor aspects of the OR, two different approaches were pursued. In the first approach, T reflexes were evoked at 100 ms after stimulus onset in a repetition-change paradigm to investigate whether T reflex amplitude would show response decrement, recovery, and dishabituation. In the first repetition-change experiment, the change comprised a difference in stimulus intensity either from 70 dB to 85 dB or from 85 dB to 70 dB. In the second repetition-change experiment, all auditory stimuli had an intensity of 70 dB. The deviant stimulus differed in a qualitative fashion (a difference in pitch) from the habituation stimulus. In addition, stimulus relevance (relevant vs. irrelevant) and interstimulus interval (2.5 s vs. 7.5 s) were manipulated.

In the second approach, T reflexes were evoked at different time lags after stimulus onset (100, 200, 300, 400, 500 ms) in an oddball paradigm in order to examine the time course of changes in the motor system induced by an attended or ignored change in pitch.

5.3 EXPERIMENT 1

In the first experiment, tendon reflexes were evoked at a lag of 100 ms from stimulus onset. A series of 21 simple auditory stimuli was presented. The deviant tone at position 20 was of either a higher or lower intensity than the habituation stimulus. The decrement of T reflex amplitude over the first 19 trials, recovery to the deviant, and dishabituation to the renewed presentation of the habituation stimulus were studied.

5.3.1 Method

Participants

Participants were 16 female and 2 male paid volunteers with a mean age of 22.1 years (range 19–31). In advance of the experiment, participants were questioned about their sense of hearing. No one reported any hearing problems.

Procedure

Stimuli were 2000-Hz tones of 50 ms duration with no rise/fall time, produced by a sinus generator and presented via a speaker (Philips box 420 car speaker) that was positioned on the ground in front of the participant at a distance of 2 meters from the participant's head. Participants were presented 19 habituation stimuli, followed by one deviant and one habituation stimulus. The interstimulus interval (ISI) was 10 s. For half of the participants a 70 dB (A) tone served as the habituation stimulus and a 85 dB (A) tone as the deviant. For the other half the 85 dB (A) tone served as the habituation stimulus and the 70 dB (A) tone as the deviant. Participants were instructed to listen to the stimulation without responding to it in any way.

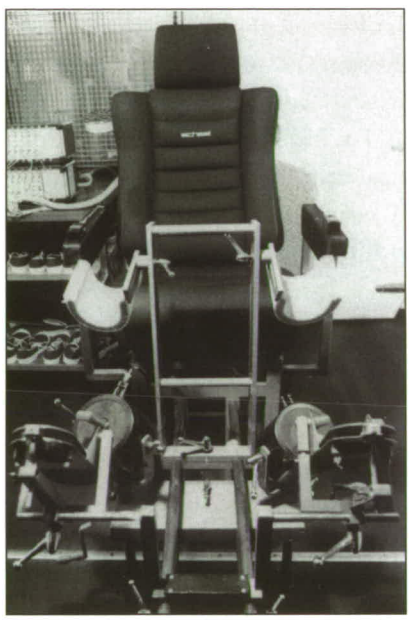

Figure 5.1. Chair specially designed to evoke T reflexes.

Physiological recording and scoring

The experiment took place in a sound attenuated and electrically shielded room. Participants were seated in a chair that was specially designed to evoke T reflexes (see Figure 5.1). The upper legs rested on braces and the feet were placed in foot supports. The posture of the legs and feet was adjusted so that the knees were positioned at an angle of 110 degrees flexion and the feet at 90 degrees flexion. T reflexes were evoked at the level of the lateral malleolus of the right Achilles tendon by means of a vibration exciter (Brüel and Kjær 4809). The vibration exciter was triggered by a 20 ms rectangular pulse, produced by a Brüel and Kjær 2706 power amplifier, of which the amplitude could be adjusted to control the magnitude of the reflex stimulus. T reflex EMG potentials were recorded from the distal part of the soleus muscle by two Ag/AgCl

surface electrodes with a contact area of 9 mm at an interelectrode distance of 3 cm. The common reference electrode was placed 4 cm above the right knee. The signals were amplified 4000 times, filtered with a 4–500 Hz bandwidth, and sampled at a rate of 2000 Hz. T reflexes were evoked at 100 ms after stimulus onset. Before and after the stimulus series, 10 T reflexes without the preceding auditory stimulus were evoked at intervals of 10 s. These T reflexes served as baseline for those evoked in the stimulus series. T reflex amplitude was determined by taking the absolute span between the positive and the negative maximum of the reflex potential in the time window of 20–70 ms after the tendon tap. T reflex amplitude of the test trials (trials including the auditory stimulus presentation) was expressed as a percentage of mean baseline T reflex amplitude.

Before the start of the experiment a number of reflexes were evoked at intervals of 10 s during which the magnitude of the reflex stimulus was adjusted. Although each participant was seated in the same position and the vibration exciter was located at the same place on the tendon, an identical magnitude of the reflex stimulus does not necessarily lead to identical T reflex amplitudes for each participant. To standardize T reflex amplitude between participants, T reflex amplitudes were monitored and the amplitude of the vibration exciter was adjusted so that each participant had initially about the same T reflex amplitude.

Statistical analysis

To test response decrement over the first 19 habituation stimuli, T reflex amplitudes were transformed into linear and quadratic polynomial terms. The linear and quadratic trend scores were subjected to statistical analyses using a multivariate analysis of variance (MANOVA) for repeated measures. Planned contrasts between the last habituation stimulus (predeviant) and the deviant stimulus, and between the predeviant and the habituation stimulus subsequent to the deviant stimulus (postdeviant) were carried out to test recovery and dishabituation, respectively. All analyses included the between-subjects factor Stimulus Intensity (70 dB vs. 85 dB). A significance level of 5% was adopted in all statistical analyses. One-tailed tests were used because response decrement to repeated presentation of identical stimuli, recovery to the deviant, dishabituation to renewed presentation of the habituation stimulus, and larger amplitudes to the 85 dB than to the 70 dB tone were a priori expected.

5.3.2 Results and discussion

First, it was tested whether auditory stimulation resulted in enhanced overall T reflex amplitudes. T reflex amplitude during the test trials was enhanced relative to mean baseline T reflex amplitude, $F(1,16) = 50.57$, $p < .001$. Stimulus Intensity did not have a significant effect on T reflex amplitude for the habituation trials. T reflex amplitude curvilinearly decreased across trials, linear trend $F(1,16) = 46.67$, $p < .001$; quadratic trend $F(1,16) = 7.50$, $p < .05$. Response decrement was not significantly affected by Stimulus Intensity. As illustrated in Figure 5.2, T reflex amplitude continued to

decrease until about trial 9. There was no main effect of recovery. Recovery of T reflex amplitude to the deviant tone depended on Stimulus Intensity, $F(1,16) = 8.78, p < .01$. As apparent from Figure 5.2, only when the deviant stimulus was of higher intensity than the habituation stimulus, recovery was significant, $F(1,8) = 9.92, p < .05$. Dishabituation of T reflex amplitude occurred independently of stimulus intensity, $F(1,16) = 7.82, p < .01$.

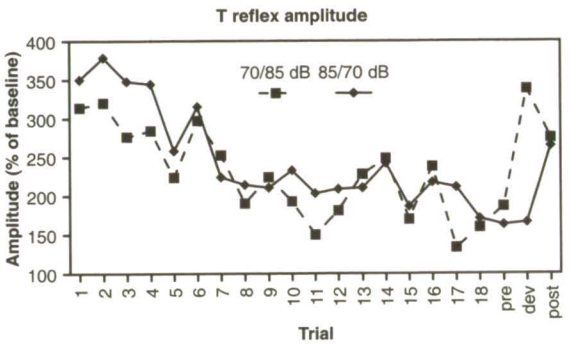

Figure 5.2. Mean T reflex amplitude across trials (pre = predeviant; dev = deviant; post = post-deviant); 70/85 dB = habituation stimulus of 70 dB, deviant stimulus 85 dB; 85/70 dB = habituation stimulus of 85 dB, deviant stimulus 70 dB.

In summary, audiospinal facilitation displayed at least two characteristics of the OR, namely response decrement and dishabituation. Recovery was found only when the deviant stimulus had a higher intensity than the habituation stimulus. The lack of recovery to an intensity decrease refutes the hypothesis that the audiogenic facilitation of T reflex amplitude is a motor component of the OR because the model-comparator theory of Sokolov (1963) predicts recovery of the OR in this situation. The dual-process theory of Groves and Thompson (1970), on the other hand, predicts a small and less reliable response to a decrease in stimulus intensity compared to an increase in intensity. The finding that recovery is affected by stimulus intensity has been substantiated in earlier studies on the SCR-OR. In repetition change paradigms, recovery to a deviant stimulus of lower intensity has not been unequivocally found. Whereas some studies found recovery of the SCR-OR to an intensity decrease (Edwards 1975; Rust, 1976; Siddle & Heron, 1977), others reported an absence of recovery of the SCR-OR to the insertion of an intensity decrease (Bernstein, 1968, 1969; James & Hughes, 1969; O'Gorman, Mangan, & Gowen, 1970). It is generally acknowledged that the lack of recovery of the SCR-OR to an intensity decrease causes embarrassment for the model-comparator theory (Bernstein, 1969; O'Gorman et al., 1970). The fact that recovery of T reflex amplitude was absent to an intensity decrease, may have been caused by the influence of absolute stimulus intensity on reflex amplitude. As SCR (Barry & Furedy, 1993), spinal reflex amplitude is positively related to the absolute stimulus intensity (Davis & Beaton, 1968; Scheirs & Brunia, 1982). Therefore, recovery of T reflex amplitude to the intensity in-

crease and the lack of recovery to the intensity decrease may in part be explained by the positive relationship between stimulus intensity and T reflex amplitude. However, this phenomenon cannot completely account for the results because in the current study there was no significant effect of stimulus intensity on T reflex amplitude for the habituation trials, not even for the very first trials, when tested (in Figure 5.2 T reflex amplitude to the first 4 trials seemed to be larger to the loud tone than to the soft tone). As an alternative explanation, recovery may be the consequence of a violation of the neuronal model of the habituation stimulus. However, in that case recovery would be expected to an intensity decrease as well. It is conceivable that both the positive effect of stimulus intensity on T reflex amplitude and the renewed novelty of the stimulus act in an interactive fashion on the recovery of T reflex amplitude to an intensity increase.

As mentioned above, significant dishabituation of T reflex amplitude was found after insertion of a stimulus of either lower or higher intensity. Both dual process theory and model comparator theory predict dishabituation after an intensity *increase*. However, the dual process cannot explain dishabituation of T reflex amplitude after an intensity *decrease* because it predicts dishabituation only following arousing deviants.

The discussion of the results demonstrates that an intensity change poses a problem for interpreting recovery and dishabituation of T reflex amplitude as reflections of a violation of the neuronal model of the stimulus because of the activating effects that are intrinsically linked to intensity modulations. Because the activity of the motor system, indexed by T reflexes, is sensitive to the intensity of auditory stimulus presentation, the activating effects of the intensity change may obscure the response of the motor system to the *novelty* of the stimulus change. These activating effects may be strengthened by the fact that the auditory stimuli had no rise and fall times, running the risk of evoking startle responses. To counteract these confounding effects of stimulus intensity and rise/fall times on recovery and dishabituation, a second experiment was conducted. It was studied whether T reflex amplitude would show recovery and dishabituation when the deviant stimulus was *qualitatively* different from the habituation stimulus. In addition, rise and fall times were inserted to lower the probability of eliciting startle reflexes.

5.4 EXPERIMENT 2

Although the main objective of Experiment 2 was identical to that of Experiment 1, that is, to study habituation[1] of T reflex amplitude, Experiment 2 differed in several respects from Experiment 1. Instead of a quantitative change, a qualitative change (change in pitch) was inserted into the habituation series. A second difference was that the stimulus series was repeatedly presented (11 times). Response scores were ordinally averaged according to the procedure originally introduced by Ritter, Vaughan, and Costa (1968) resulting in a higher signal to noise ratio of the response scores. The effects

1 The term "habituation" is used to indicate the inferred process underlying the observed changes, and includes response decrement, recovery, and dishabituation of the OR.

of stimulus significance and interstimulus interval on the habituation of T reflex amplitude were also studied, because in previous studies habituation of the OR was affected by these two manipulations (see chapter 3). If T reflex amplitude would be affected by these manipulations, this would strengthen the hypothesis that audiospinal facilitation is an OR-mediated response. Additionally, it was studied whether decrement, recovery, and dishabituation of T reflex amplitude would run in parallel with decrement, recovery, and dishabituation of a cerebral index (N100) of the OR. Such a congruency is of interest because the nonspecific N100 and the facilitation of T reflex amplitude to an auditory stimulus may be functionally related, that is, share a common generator and display the same underlying mechanism. It could be argued that parallel habituation of the nonspecific N100 and audiospinal facilitation reflects the integrated response within the unitary OR process. Näätänen and Picton (1987) proposed a common underlying mechanism for the nonspecific N100 and audiospinal facilitation. The nonspecific N100 is probably generated in the frontal motor and premotor cortex under influence of the reticular formation and reaches its maximum at the vertex (Näätänen & Picton, 1987). These authors suggested that the discharge of the neuronal population underlying the nonspecific N100 component triggers a widespread transient arousal burst facilitating sensory and, in particular, motor responses. Support for this hypothesis is the alleged functional relationship between the nonspecific N100 and activity in the motor system. A number of different findings point to such an interrelationship. First, manipulation of certain stimulus variables affects the N100 and spinal reflexes in the same way. Both the N100 (Näätänen, 1992) and spinal reflexes (Davis & Beaton, 1968; Scheirs & Brunia, 1982) show a positive relationship between tone intensity and response magnitude. Second, rise time effects have been demonstrated in both N100 and T reflexes. Decreasing rise time caused an increase in amplitude of both the nonspecific component of the N100 (Loveless & Brunia, 1990) and T reflexes (Brunia, 1993). Another demonstration of the relationship between the N100 and activity in the motor system came from Hazemann, Audin, and Lille (1975). Their study showed that during voluntary self-paced movements the auditory N100 was reduced. Näätänen and Picton (1987) suggested that the enhancement of spinal reflexes to an auditory stimulus may be mediated by descending influences from the reticular formation and the frontal cortex. If both the nonspecific N100 and the motor facilitation really arise from the mesencephalic reticular formation (MRF), specific predictions can be made about motor facilitation during the OR because the MRF is supposed to be involved in the production of the OR (Sokolov, 1960, 1963). In Sokolov's model-comparator theory, activation of the MRF elicits autonomic (SCR) and somatic components of OR. Stimulus repetition leads to the formation of a neuronal model in the cortico-hippocampal circuit and thereby to inhibition of the MRF. Considering the involvement of MRF in motor facilitation as a response to (novel) stimuli and the role of the MRF in the OR, parallel habituation of T reflex amplitude, SCR, and the N100 may be predicted. Therefore, the aim of the current experiment was to examine response

decrement, recovery, and dishabituation of SCR, N100, and T reflexes to auditory stimuli.

Besides the possible covariation between habituation of reflex facilitation and the N100, the study of the habituation of the N100 in itself is interesting. In chapter 3 it was extensively discussed whether decrement of the N100 to iteration of identical stimuli is caused by the loss of novelty or whether it is the result of refractoriness of the neural generators of the N100. When the N100 would show recovery and dishabituation, this would support the habituation hypothesis. It was already noted that, although there are several studies on the "habituation" of the N100, only a few studies tested recovery of the N100, and even fewer studies tested for dishabituation. The current study contributes to the understanding of the habituation of the N100 because it incorporates a test for recovery as well as for dishabituation. Recovery and dishabituation of the N100 have not been unequivocally found in STA (short-term averaging) designs (see sections 3.2.3 and 3.2.4 for a more elaborated discussion of recovery and dishabituation of the N100). A possible cause might be that recovery and dishabituation of the N100 decrease across stimulus series, reducing the magnitude of recovery and dishabituation in the ordinal average. Kenemans, Verbaten, Roelofs, and Slangen (1989) demonstrated that recovery of the N100 indeed declined with repeated presentation of a visual deviant stimulus. In the current experiment, it was therefore examined whether recovery and dishabituation of N100 amplitude would show a gradual decrease across stimulus series.

In addition to the failure to unequivocally demonstrate recovery and dishabituation, the morphology of the decrement of the N100 has led some investigators to believe that the observed decrement is not the result of an inferred habituation process but stems from refractoriness of the neural generators of the N100 (e.g., Budd et al., 1998; Näätänen, 1992; Ritter et al., 1968). In STA designs, the decrement of the N100 often reaches an asymptotic level at the second trial, especially with short interstimulus intervals. This pattern would be expected from a response system that is in some state of refractoriness (Budd et al., 1998). However, it can be counterargued that the very fast decrement may develop over the repeated stimulus series. In the first series, the N100 might decrease slower compared to the ordinal averages because stimuli are presented for the first time and therefore contain a high degree of novelty. As stimulus series – with large interseries intervals with respect to ISI – are repeatedly presented, only the first stimulus of a series contains novelty because of a higher time uncertainty compared to the ensuing stimuli in that series. Because time uncertainty has a large influence on the occurrence of the N100 (Bourbon et al., 1987; Näätänen & Picton, 1987), very fast decrement of the N100 in STA studies is indeed to be expected. Thus, if the decrement of the N100 is not caused by refractoriness of the neural generators of the N100, it is expected to be less fast to the very first stimulus presentations in an STA experiment because these stimuli still possess a high novelty/time uncertainty. In short, the argument is that the morphology of the decrement of the N100 may be influenced by the ordinal averaging technique. Therefore, in the current experiment the decrement of the

N100 obtained by ordinal averaging was compared with the decrement of the N100 to the stimulus presentations in the first series, using single trial estimates (using OPTA: Woestenburg, Verbaten, Van Hees, & Slangen, 1983) of the N100.

In addition to the habituation of the SCR, N100, and T reflex amplitude, habituation of the P3 was examined as well. In OR literature it has been suggested that the P3 can be regarded as a central index of the OR (see section 3.4). However, it is unclear whether the P3 decreases as fast as the SCR and N100 in repetition-change paradigms. In a study of Verbaten, Roelofs, Sjouw, and Slangen (1986a), the visual P3 decreased more slowly than the SCR. In contrast, Simons et al. (1987) found a faster decrement of the auditory P3 than of the SCR. In addition, in some studies the P3 decreased over trials as fast as the N100 (e.g., Megela & Teyler, 1979), whereas in other studies, the decrement of the P3 was slower than that of the N100 (e.g., Verbaten et al., 1986a). In general, slow decrement of the P3 was obtained with single trial estimates using OPTA, whereas fast decrement of the P3 was found in STA designs. It is conceivable that these inconclusive results may be ascribed to the different procedures to increase the signal to noise ratio of the ERP. To test this potentially confounding factor in the current experiment, the decrement of P3 amplitude was analyzed using both ordinal averaging and single trial estimates (by means of OPTA).

5.4.1 Method

Participants

Fifty-six volunteers (38 women, 18 men) participated in the experiment. Their age ranged from 19 to 52 years with a mean age of 21.3 years. Participants received course credits or a monetary compensation. No one reported hearing or vision disorders.

Procedure

The experimental design that was used was an adaptation of the design originally introduced by Ritter et al. (1968). Participants were presented 11 blocks of auditory stimuli. A stimulus block contained at least 19 and at most 23 stimuli. In each block, habituation stimuli (pure tones of 1000 Hz) were interspersed with one deviant stimulus (pure tone of 500 Hz). The deviant stimulus was presented randomly between tone 10 and tone 17. Although, in most STA studies the position of the deviant trial is fixed, in the current experiment the position of the deviant trial was varied randomly between stimulus series to reduce the risk of habituation to the deviant tone. Both habituation stimulus and deviant stimulus had an intensity of 70 dB(A) and a duration of 50 ms with a 10-ms rise/fall time. Stimuli were produced by means of a 16 bit soundcard and were delivered binaurally through insertion headphones (Etymotics ER-2). The interblock interval ranged from 30 to 60 seconds.

There were four conditions, each containing 14 participants, determined by length of ISI (measured from stimulus onset to stimulus onset: 2.5 s vs. 7.5 s) and stimulus

relevance (stimulus relevant vs. stimulus irrelevant). In the stimulus-relevant condition, participants were instructed to pay attention to the stimuli by means of pressing a response button to every habituation stimulus that was held in the left hand. Participants were encouraged to perform button pressing with minimal force, and to react as fast and accurate as possible. A response button held in the right hand had to be pushed in response to the deviant stimulus. For half of the participants in the stimulus-relevant condition this response pattern was reversed, that is, a response was given with the right hand to the habituation stimulus and a response with the left hand to the deviant stimulus. In order to be able to make a distinction between the habituation stimulus and the deviant stimulus, participants in the stimulus-relevant condition were presented a few habituation stimuli and deviants five minutes before the onset of the experiment. It was assumed that finger flexion with minimal force would not affect T reflex amplitude, first, because reaction times were expected to be significantly longer than 100 ms (i.e., longer than the tone-reflex interval), and second, because there is no evidence for such an effect. Rudell and Eberle (1985) found that H reflex amplitude, evoked at 100 ms after tone onset, was not related to reaction time.

In the stimulus-irrelevant condition, attention was diverted from the auditory stimuli by means of a visual vigilance task (Mackworth's clock test, 1948). Participants were instructed to focus on the visual task and were told a cover-up story in which it was explained that auditory stimuli were presented concurrently with T reflexes because that would synchronize brain waves. During the task, an analog clock (visual angle = 3.74°) with one arm was displayed on a monitor. The arm made a discrete jump every second. It took 40 jumps to complete a revolution. Occasionally, the arm jumped twice the distance. This occurrence had to be counted during the experiment. The shortest interval between two double jumps was 5 single jumps. The longest interval was 26 single jumps. In essence, Mackworth's clock test is an oddball task. Double jumping of the arm may well elicit a P3. To prevent contamination of the auditory ERP with a visual P3, it was arranged that double jumping took place only outside the interval of 1 s before to 1 s after auditory stimulus presentation.

Physiological recording and scoring

Electrodermal activity (EDA) was recorded using a constant voltage (.5 V) EDA-coupler with two Ag/AgCl electrodes (contact area of 8 mm) placed under the left foot, according to the guidelines of Boucsein (1992). The electrolyte medium contained a .05-M concentration of NaCl in Unibase. EDA was filtered (DC to 8 Hz) and sampled at 1000 Hz by a 12 bit AD converter. Because of the relative short ISIs, the traditional baseline-to-peak measurement was inadequate because SCR did not return to baseline before the next trial, which might lead to an underestimation of the response amplitude and even to scoring of a zero response (cf. Barry et al., 1993). To deal with this problem a procedure of Barry et al. (1993) was applied. In this procedure, the falling slope of a response was linearly extended below the peak of the response belonging to the next

trial. SCR amplitude was calculated as the vertical distance between the peak and the intersection of a vertical projection from the peak to the abscissa (time-axis) and the linear extrapolation of the falling slope (see Figure 5.3). SCR amplitudes of trials 1 to 9 of every block were ordinally averaged over the 11 blocks. In addition, SCR amplitudes of the last habituation stimulus (predeviant), the deviant stimulus, and the habituation stimulus immediately following the deviant (postdeviant) were averaged.

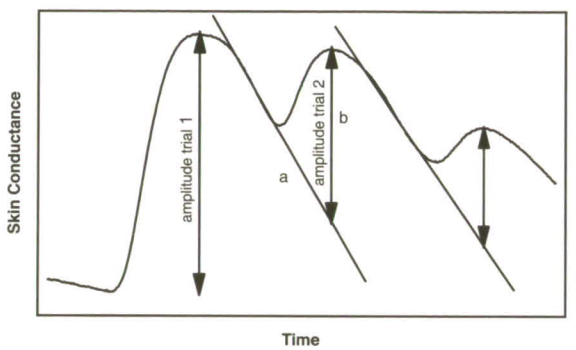

Figure 5.3. Scoring of SCR amplitude indexed by the double-headed arrows (a = extrapolation of falling slope; b = vertical projection from peak to the time-axis).

ERPs following auditory stimuli were recorded with Ag/AgCl electrodes from the following locations: F3, Fz, F4, C3, Cz, C4, T3, T4 and Pz (according to the 10-20 system). All electrodes were referenced to the algebraic average of left and right mastoids. Electrode impedance was always lower than 3Ω. The time constant of the EEG amplifier was 1 s, the low pass filter 30 Hz. EEG was sampled at a rate of 1000 Hz. Horizontal EOG was recorded from electrodes placed at the outer canthi of both eyes. Vertical EOG was recorded for both eyes with electrodes placed 1 cm above the eyebrow and 1 cm below the eye on a vertical line through the pupil. Before the start of the experiment, an eye movement calibration trial was recorded, allowing to estimate correction parameters that were used to correct the EEG for eye movement artifacts (cf. Van den Berg-Lenssen, Brunia, & Blom, 1989). A prestimulus EEG record ranging from 300 ms to stimulus onset served as baseline for the scoring of ERP amplitudes. Two ERP amplitudes were scored: the N100 and the P3. The N100 was scored as the amplitude of the first negative peak between 50 and 150 ms after stimulus onset, the P3 as the amplitude with the largest positive peak between 250 ms and 550 ms. Two different approaches were applied to enhance the signal to noise ratio. First, ERPs of trials 1 to 9 of every block were ordinally averaged over the 11 blocks. In addition, ERPs to the predeviant, deviant, and postdeviant stimuli were averaged. In the second approach, ERPs were analyzed on a single-trial basis. Single trial estimates were determined by an orthogonal polynomial trend analysis (OPTA, Woestenburg et al., 1983). The first 14 habituation stimuli of the first block were entered into OPTA (the

first stimulus block always contained at least 14 habituation stimuli). Analysis of response decrement was performed over the first 9 trials of the first block. Additionally, ERPs to the predeviant, deviant, and postdeviant stimuli of the 11 blocks were entered into OPTA yielding 3 series of 11 single trial ERPs. The latter procedure allowed us to detect a possible decrement of the recovery and dishabituation of the ERPs.

T reflexes were evoked at 100 ms after tone onset. Before the first and after the last stimulus block, 10 T reflexes without a preceding auditory stimulus were evoked at a rate corresponding to the ISI in the stimulus series. In the interblock interval, T reflexes were also evoked at a rate corresponding to the ISI in the stimulus series. All T reflexes without the preceding auditory stimuli served as baseline (100%) for T reflexes evoked in the tone series. T reflex amplitude was computed by determining peak-to-peak amplitude. T reflex amplitudes of trials 1 to 9 of every block were ordinally averaged over the 11 blocks. In addition, T reflex amplitudes of the predeviant, deviant, and postdeviant trials were averaged.

Statistical analysis

During data analysis of the SCR it was discovered that only SCR amplitude in the long-ISI condition could be scored. In the short-ISI condition, the SCR of individual trials did overlap to such an extent that no maximum of the SCR belonging to a particular trial could be discerned. That is, electrodermal activity of a particular trial was still rising at the onset of the next trial. Hence, scoring of a maximum was impossible. Therefore, results concerning the SCR were confined to the long-ISI condition.

In addition to the physiological measures, reaction times (ordinal averages) to the tones in the stimulus-relevant condition were examined as well. Although the overt response was meant to manipulate stimulus relevance and was not object of the study originally, it can be considered a behavioral index of the OR.

Ordinal averages of the first nine trials of reaction time, SCR, N100, P3, and T reflex amplitude were entered into a multivariate analysis of variance (MANOVA) for repeated measures. Response decrement was analyzed by testing the linear and quadratic trends over trials 1 to 9. In addition to the linear and quadratic trends, statistical analysis comprised the factor Stimulus Relevance (relevant vs. irrelevant) for SCR, N100, P3, and T reflex amplitude. The factor ISI (2.5 s vs. 7.5 s) was included for reaction time, N100, P3, and T reflex amplitude. The factor Lead (F3, Fz, F4, C3, Cz, C4, T3, T4, Pz) was included for N100 and P3. A similar analysis was carried out to examine response decrement of the single trial ERPs (OPTA N100 and OPTA P3) over the first nine trials of the first stimulus block.

Planned contrasts between the predeviant and the deviant stimulus, and between the predeviant and the postdeviant stimulus were performed for reaction time, SCR, N100 (only ordinal averages), P3 (only ordinal averages), and T reflex amplitude to test recovery and dishabituation, respectively.

To examine a possible habituation of recovery of the N100, for each stimulus block

the OPTA N100 amplitude to the predeviant trial was subtracted from the amplitude to the deviant trial. Subsequently, the linear and quadratic trends of these difference scores over stimulus blocks were tested. To examine habituation of dishabituation, trends were tested for the difference between OPTA N100 amplitudes of postdeviant and predeviant trials.

A significance level of 5% was adopted in all statistical analyses. Linear and quadratic trends, recovery, dishabituation, and the main effects of Stimulus Relevance and ISI were tested using one-tailed tests because of directional predictions. It was expected that amplitudes of N100, P3, and T reflex would be lower in the short-ISI condition than in the long-ISI condition. Finally, amplitudes of N100, P3, SCR, and T reflex were expected to be higher in the stimulus-relevant condition than in the stimulus-irrelevant condition.

5.4.2 Results

Response decrement

Reaction time. As shown in Figure 5.4, reaction time decreased curvilinearly over trials, linear trend $F(1,26) = 144.65$, $p < .001$; quadratic trend $F(1,26) = 166.56$, $p < .001$. The linear trend was affected by ISI, $F(1,26) = 5.87$, $p < .05$. The linear trend in the long-ISI condition was stronger, $F(1,13) = 93.18$, $p < .001$, than in the short-ISI condition, $F(1,13) = 52.18$, $p < .001$. As shown in Figure 5.4, the decrement of reaction time in the long-ISI condition was delayed compared to that in the short-ISI condition. Reaction times in the long-ISI condition were significantly longer than in the short condition, $F(1,26) = 3.48$, $p < .05$.

SCR. Both the linear and quadratic trends of SCR were significant, $F(1,26) = 29.26$, $p < .001$; $F(1,26) = 12.18$, $p < .01$, and were not influenced by Stimulus Relevance. Although Figure 5.4 points to a main effect of Stimulus Relevance on SCR amplitude, this effect was not significant.

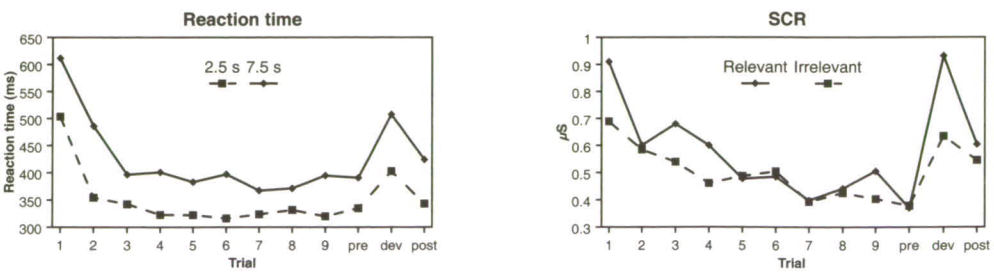

Figure 5.4. Decrement, recovery, and dishabituation of mean reaction time and mean SCR (pre = predeviant; dev = deviant; post = postdeviant). Results of SCR are depicted only for the long-ISI condition.

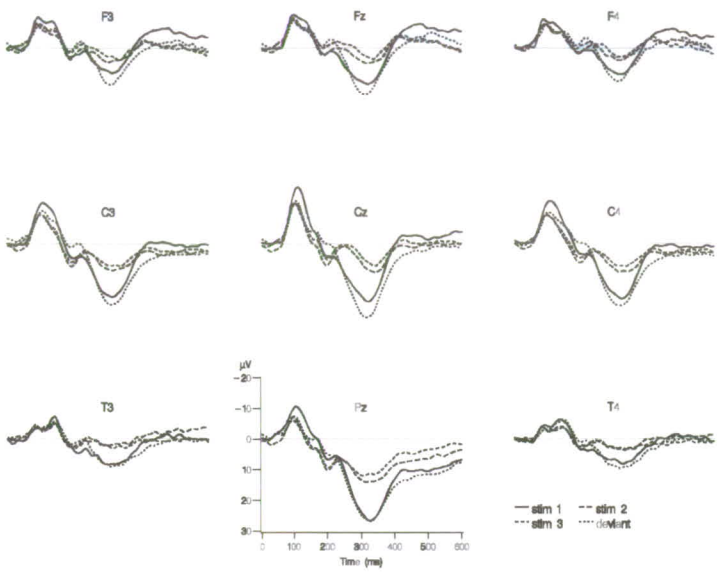

Figure 5.5. Ordinally averaged ERPs in the stimulus-relevant condition.

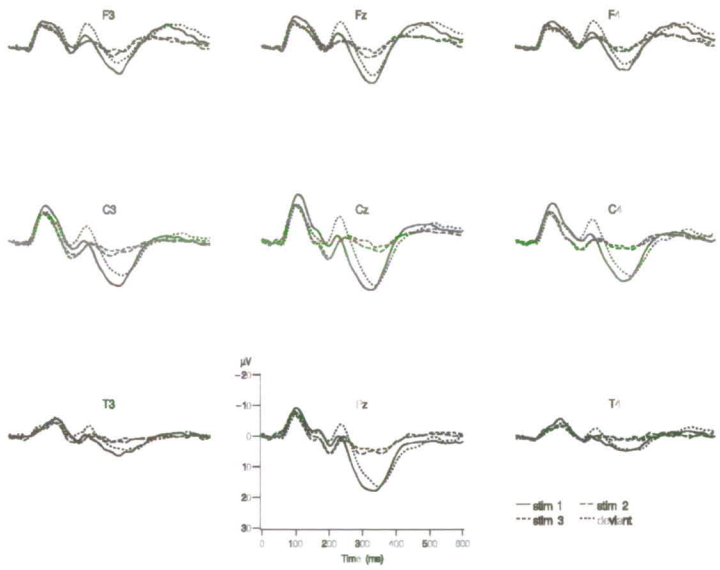

Figure 5.6. Ordinally averaged ERPs in the stimulus-irrelevant condition.

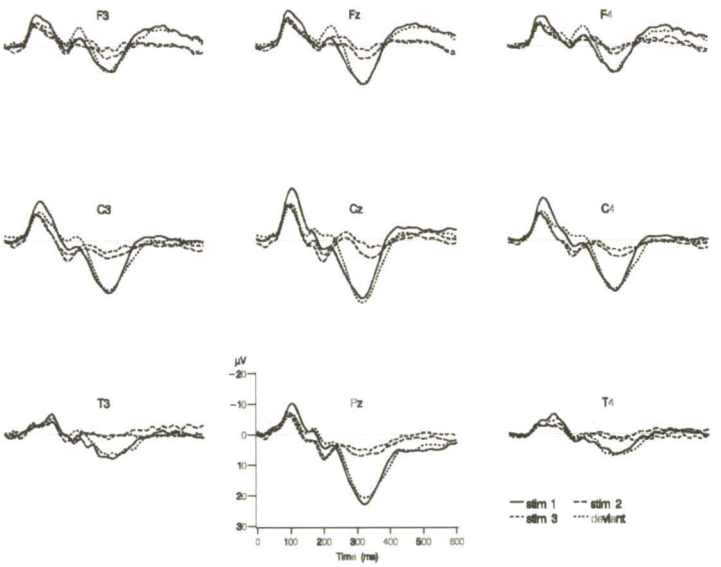

Figure 5.7. Ordinally averaged ERPs in the short-ISI condition.

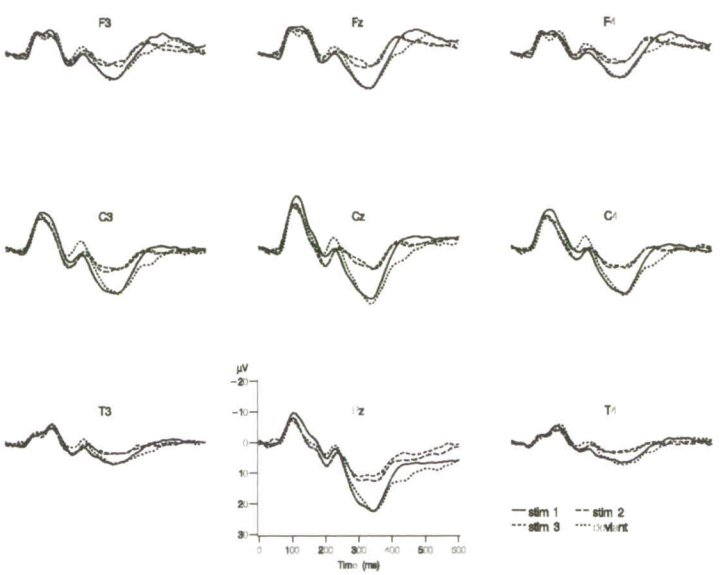

Figure 5.8. Ordinally averaged ERPs in the long-ISI condition.

Event related potentials. Figures 5.5 to 5.8 present the ordinally averaged ERPs of trials 1, 2, 3, and the deviant trial for both ISI and stimulus relevance conditions. These figures are intended to show the scalp distribution, decrement (over the first three trials), and recovery of the ERPs at all electrode positions. Additional figures (5.9 and 5.10) are presented, providing a better insight in the decrement of the ERP amplitudes across trials. In these figures, the amplitudes of N100 and P3 are plotted only at Cz and Pz, respectively, because these ERP components reached their maximum at these electrode positions. Figure 5.9 shows the amplitudes of the ordinally averaged N100 and OPTA N100. Figure 5.10 shows the amplitudes of the ordinally averaged P3 and OPTA P3.

Ordinally averaged N100. As Figure 5.9 indicates, the N100 showed a curvilinear decrement, linear $F(1,52) = 55.37, p < .001$; quadratic $F(1,52) = 18.29, p < .001$. The linear and quadratic trends significantly varied with electrode positions, $F(8,45) = 4.95, p < .001$; $F(8,45) = 2.20, p < .05$. The linear trends were found at all electrode positions (F ratios varied between 13.90 and 66.29), whereas the quadratic trends were significant at F3, C3, Cz, C4, T3, T4, and Pz (F ratios varied between 5.61 and 20.64), but not at Fz and F4. The linear and quadratic trends were significantly influenced by ISI, linear $F(1,52) = 6.34, p < .05$; quadratic $F(1,52) = 10.66, p < .01$, but not by Stimulus Relevance. The linear decrement in the short-ISI condition, $F(1,52) = 60.84$, $p < .001$, was more significant than in the long-ISI condition, $F(1,52) = 9.71, p < .01$. The quadratic decrement was only significant in the short-ISI condition, $F(1,52) = 33.26, p < .001$.

N100 amplitude in the long-ISI condition was enhanced compared to that in the short-ISI condition, $F(1,52) = 4.16, p < .05$. Stimulus Relevance had no significant main effect on N100 amplitude. However, at Cz there was an ISI x Stimulus Relevance interaction, $F(1,52) = 4.15, p < .05$. Simple effect tests revealed that in the long-ISI condition, N100 amplitude at Cz was larger when the stimulus was relevant than when it was irrelevant, $F(1,26) = 4.97, p < .05$.

OPTA N100. Figure 5.9 displays the OPTA N100 as function of the first nine trials. The OPTA N100 decreased both linearly and quadratically, $F(1,52) = 15.9, p < .001$; $F(1,52) = 15.40, p < .001$. Neither ISI nor Stimulus Relevance significantly affected the linear and quadratic trends. The linear and quadratic trends did not vary with Lead.

OPTA N100 amplitude was larger in the long-ISI condition than in the short-ISI condition, $F(1,52) = 4.64, p < .05$. No main effect of Stimulus Relevance on OPTA N100 amplitude was found.

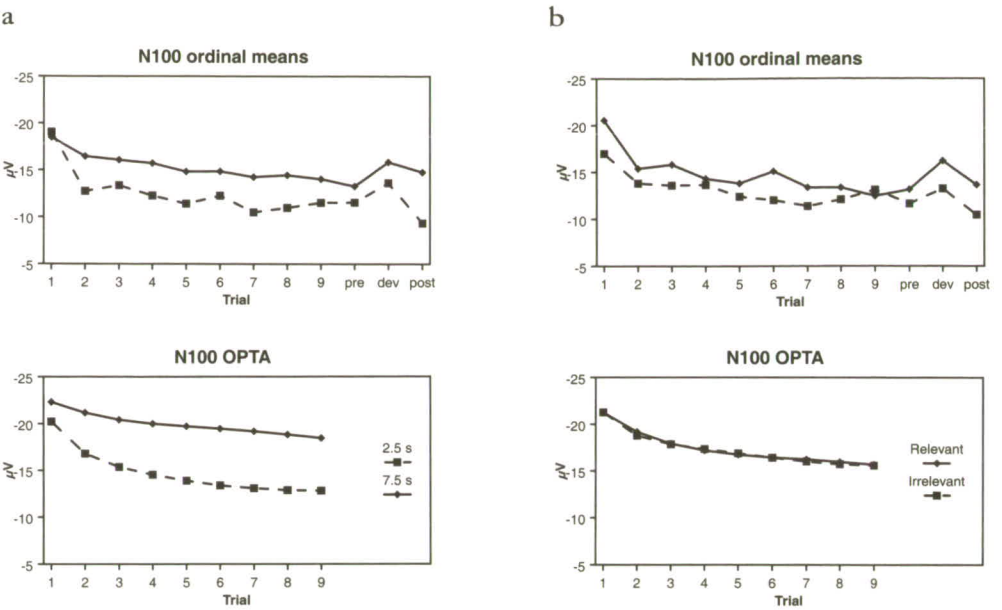

Figure 5.9. Decrement, recovery, and dishabituation of the N100 at Cz (pre = predeviant; dev = deviant; post = postdeviant) in the short-ISI and long-ISI conditions (a), and in the stimulus-relevant and stimulus-irrelevant conditions (b).

In summary, both the ordinally averaged N100 and OPTA N100 decreased curvilinearly across identical stimulation trials. The decrement of the N100 was faster with short ISIs than with long ISIs. Both the ordinally averaged N100 and OPTA N100 amplitudes were larger in the long-ISI condition than in the short-ISI condition. In neither case, Stimulus Relevance had an effect on the decrement of the N100. Stimulus Relevance had no main effect on the ordinally averaged N100 or OPTA N100 amplitude. However, the results of the ordinal averaging procedure showed that with long ISIs, N100 amplitude at Cz was larger when the stimulus was relevant.

Ordinally averaged P3. As illustrated in Figures 5.5 to 5.8, P3 amplitude had a parietal maximum. The P3 showed a linear, $F(1,52) = 130.37$, $p < .001$, and quadratic decrement, $F(1,52) = 82.80$, $p < .001$ (Figure 5.10). Although the linear and quadratic trends differed between electrode positions, $F(8,45) = 6.84$, $p < .001$, and $F(8,45) = 5.03$, $p < .05$, respectively, both the linear trends (F ratios varied between 10.95 and 137.12) and quadratic trends (F ratios varied between 16.06 and 135.46) were significant at every lead. The linear and quadratic trends were not affected by ISI or Stimulus Relevance.

Both ISI, $F(1,52) = 4.43$, $p < .05$, and Stimulus Relevance affected P3 amplitude, $F(1,52) = 20.51$, $p < .001$. As apparent from Figure 5.10, P3 amplitude was larger in the long-ISI condition than in the short-ISI condition, and larger in the stimulus-relevant condition than in the stimulus-irrelevant condition.

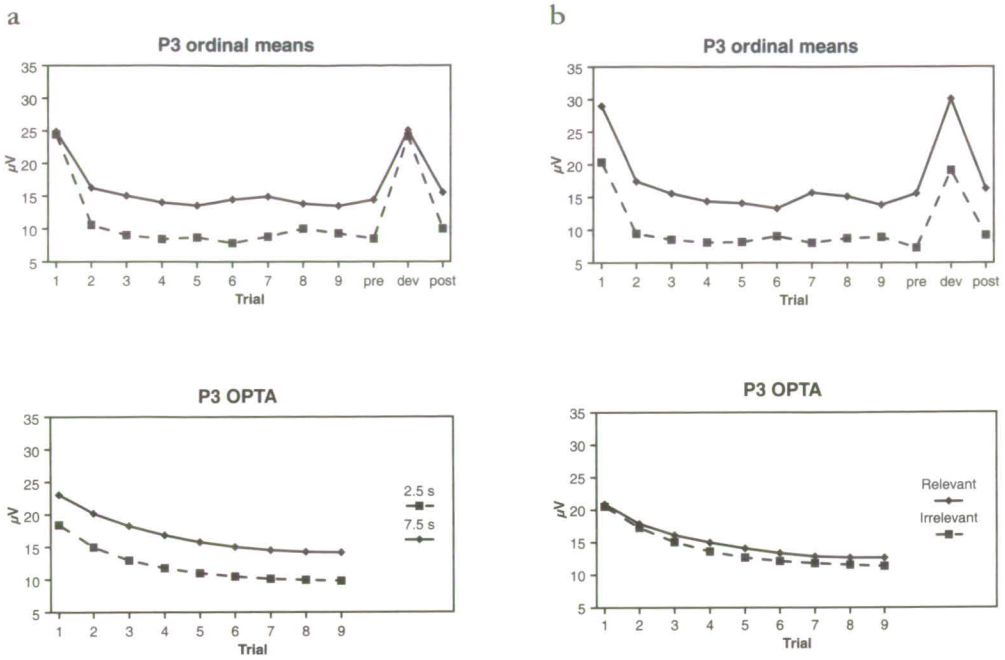

Figure 5.10. Decrement, recovery, and dishabituation of the P3 at Pz (pre = predeviant; dev = deviant; post = postdeviant) in the short-ISI and long-ISI conditions (a), and in the stimulus-relevant and stimulus-irrelevant conditions (b).

OPTA P3. The linear, $F(1,52) = 67.56, p < .001$, and quadratic decrement, $F(1,52) = 71.63, p < .001$, of the OPTA P3 were independent of ISI and Stimulus Relevance (Figure 5.10). Although the linear trend was significant at every electrode position, $F(8,45) = 2.38, p < .05$, it varied with Lead (F ratios varied between 6.39 and 49.47). The quadratic trend did not differ between electrode positions.

ISI and Stimulus Relevance had no main effects on P3 amplitude. There was, however, an ISI x Stimulus Relevance interaction, $F(1,52) = 11.44, p < .01$. Simple effect tests revealed that P3 amplitude was larger when the stimulus was relevant compared to when it was irrelevant in the short-ISI condition, $F(1,26) = 8.71, p < .01$. In addition, when the stimulus was irrelevant, P3 amplitude was larger in the long-ISI condition than in the short-ISI condition, $F(1,26) = 13.86, p < .01$. When the P3 was analyzed only at Pz, P3 amplitude was larger in the long-ISI condition than in the short-ISI condition, independently of Stimulus Relevance, $F(1,52) = 6.88, p < .05$.

In summary, both the ordinally averaged P3 and OPTA P3 clearly showed a curvilinear decrement that was not influenced by ISI or Stimulus Relevance. The STA procedure yielded larger P3 amplitudes in the long-ISI condition compared to the short-ISI condition, and larger amplitudes in the stimulus-relevant condition as opposed to the stimulus-irrelevant condition. In the first stimulus block, the expected effect of stimulus

relevance on OPTA P3 amplitude existed only when ISI was short. The expected effect of ISI on OPTA P3 amplitude was found only in the stimulus-irrelevant condition.

T reflex. As shown in Figure 5.11, T reflex amplitude decreased both linearly, $F(1,52) = 15.89, p < .001$, and quadratically, $F(1,52) = 4.65, p < .001$, over trials. The decrement of T reflex amplitude was not affected by ISI or Stimulus Relevance.

Although Figure 5.11 suggests larger T reflex amplitudes in the stimulus-relevant condition than in the stimulus-irrelevant condition, this difference was not significant. In addition, T reflex amplitude was not influenced by ISI. It is striking that in the stimulus-relevant condition, T reflex amplitude in the first trial is smaller than in the second trial. However, this was not a strong effect because in this condition T reflex amplitude did not differ significantly between trials 1 and 2.

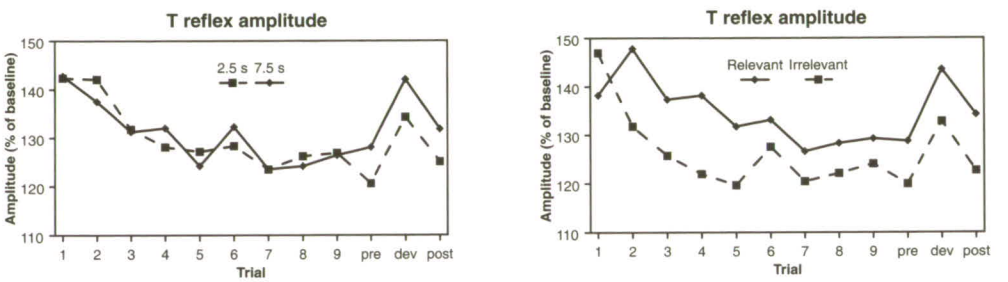

Figure 5.11. Decrement, recovery, and dishabituation of T reflex amplitude (pre = predeviant; dev = deviant; post = postdeviant) in the short-ISI and long-ISI conditions, and in the stimulus-relevant and stimulus-irrelevant conditions.

Comparison between the decrement of SCR, N100, P3, and T reflex amplitude

As illustrated in Table 5.1 and in Figures 5.4 to 5.11, both the SCR, N100, P3, and T reflex amplitude decreased in a curvilinear fashion over trials. In other words, response decrement was very similar for different response systems. In this section, the covariation of response decrement is examined in more detail. The linear and quadratic trends of different response systems were compared to examine covariation of response decrement. Considering the relevant research questions, the following comparisons were of interest: T reflex vs. N100; T reflex vs. SCR; N100 vs. SCR; and N100 vs. P3. In order to test parallel decrement across the habituation trials, response scores (only the ordinal averages were used) were first transformed into z-scores. Following this operation, ERPs, SCR, and T reflexes were measured on the same scale, making a direct comparison possible (Figure 5.12).

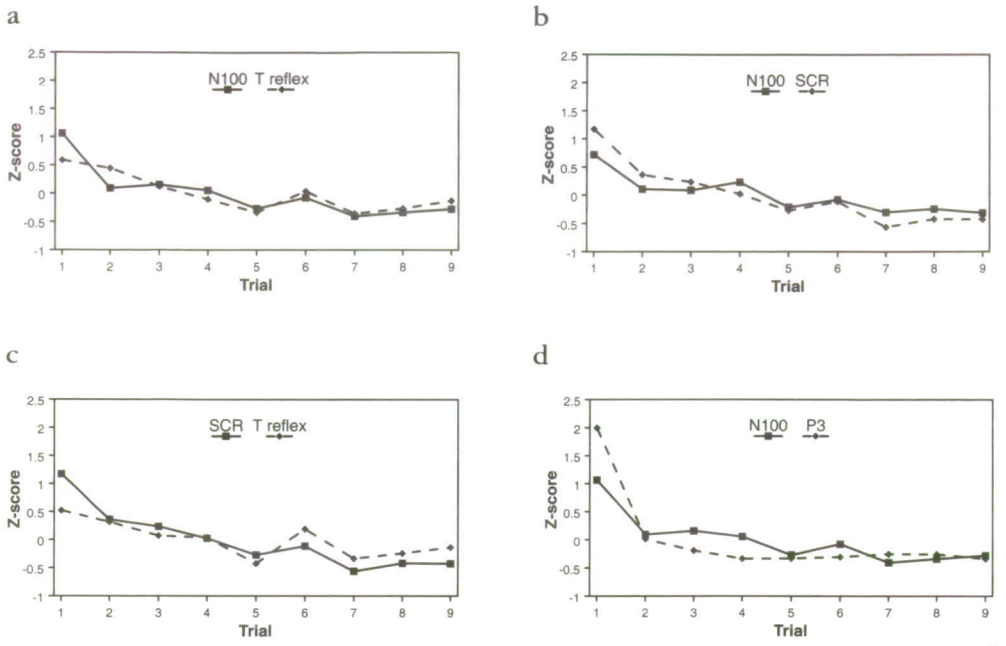

Figure 5.12. Comparison of decrement between (a) the N100 and T reflex amplitude, (b) the N100 and the SCR, (c) the SCR and T reflex amplitude, (d) the N100 and the P3. Note that comparisons concerning the SCR were carried out only in the long-ISI condition.

Note that comparisons of SCR with other response systems were done only for long ISIs. The decrement of N100 measured at electrode position Cz was compared with the decrement of the other measures because the nonspecific component of N100 is maximal at Cz. First, the linear and quadratic trends of the SCR and T reflex amplitude were compared. There was a significant difference in the linear trends, $F(1,26) = 7.15$, $p < .05$. The linear trend of the SCR was more significant, $F(1,26) = 50.64$, $p < .001$, than that of T reflex amplitude, $F(1,26) = 9.12$, $p < .01$. The quadratic trend did not differ between the SCR and T reflex amplitude. Next, the decrement of T reflex amplitude was compared to that of the N100. The linear and quadratic trends of T reflex amplitude and the N100 did not significantly differ. Comparison between the linear trend of the N100 and the linear trend of the SCR revealed that the linear trend of the N100 differed from the linear trend of the SCR, $F(1,26) = 4.90$, $p < .05$. The linear trend of the SCR was more significant, $F(1,26) = 61.77$, $p < .001$, than the linear trend of the N100, $F(1,26) = 21.99$, $p < .001$. The quadratic trends were not significantly different. Comparison of the trends of the N100 and the P3 (at Pz) revealed significant differences in the linear, $F(1,52) = 7.15$, $p < .05$, and quadratic, $F(1,52) = 9.79$, $p < .01$, trends. Both the linear, $F(1,52) = 170.26$, $p < .001$, and quadratic trends, $F(1,52) = 83.17$, $p < .001$, of the P3 were more significant than the linear, $F(1,52) = 60.90$, $p < .001$, and quadratic trends, $F(1,52) = 16.62$, $p < .01$, of the N100. These differences

could probably be attributed to the larger decrement between trials 1 and 2 for the P3 than for the N100. In spite of this difference, the morphology of the decrement of both the N100 and the P3 is quite similar. For both the N100 and the P3, the decrement occurred mainly between trials 1 and 2, followed by a small decrement across the ensuing trials.

Comparison between the decrement of the ordinally averaged and single trial N100 and P3

In the introduction of Experiment 2 it was hypothesized that the ordinal averaging technique itself might affect the morphology of the response decrement of the N100 and P3. To test this hypothesis we compared the linear and quadratic trends of the ordinally averaged N100 and P3 (z-scores) with that of the OPTA N100 and P3, respectively (see Figure 5.13). The linear and quadratic trends of the ordinally averaged N100 and the OPTA N100 were not significantly different. The linear trend of the ordinally averaged P3 was different from the linear trend of the OPTA P3, $F(1,52) = 16.30$, $p < .001$. The linear trend of the ordinally averaged P3 was more significant, $F(1,52) = 170.26$, $p < .001$, than the linear trend of the OPTA P3, $F(1,52) = 156.77$, $p < .001$. The quadratic trend of the ordinal P3 did not significantly differ from that of the OPTA P3.

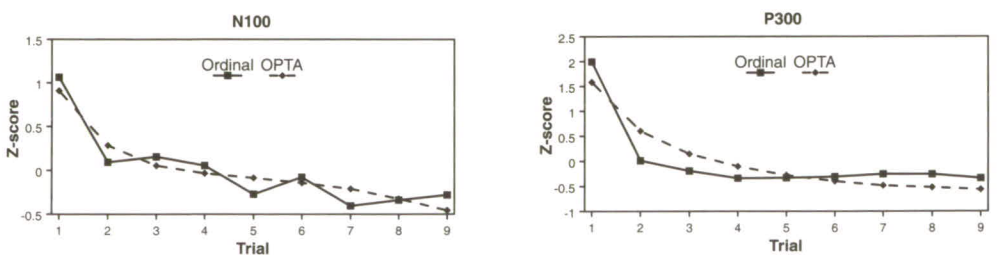

Figure 5.13. Comparison between the decrement of the ordinal averaged N100 and the decrement of the OPTA N100, and between the decrement of the ordinal averaged P3 and the decrement of the OPTA P3.

In summary, there is no evidence that the ordinal averaging procedure in itself had an effect on the decrement of the N100. In other words, the decrement of the ordinally averaged N100 was not speeded compared to the decrement of the N100 to the first series of stimulus presentations. Despite the fact that the linear trend of the ordinally averaged P3 was significantly different from that of the OPTA P3, both trends were highly significant (F ratios were higher than 100). It is therefore justified to claim that both the single trial P3 and the ordinally averaged P3 decrease at a rapid rate over a series of identical stimuli.

Table 5.1. *Summary of results of linear (lin) and quadratic (quad) trend analysis and of effects of ISI and Stimulus Relevance (Rel) for reaction time (RT), SCR, ordinally averaged and OPTA N100, ordinally averaged and OPTA P3, and T reflex amplitude*

	RT	SCR	Ordinal N100	OPTA N100	Ordinal P3	OPTA P3	T reflex
lin	+	+	+	+	+	+	+
quad	+	+	+	+	+	+	+
ISI x lin	+	0	+	–	–	–	–
ISI x quad	–	0	+	–	–	–	–
Rel x lin	0	–	–	–	–	–	–
Rel x quad	0	–	–	–	–	–	–
ISI	+	0	+	+	+	+ (Pz)	–
Rel	0	–	–	–	+	–	–
ISI x Rel	0	0	+	–	–	+	–

Note: + significant; – not significant; 0 not tested

Table 5.2. *Summary of recovery and dishabituation of reaction time (RT), SCR, N100, P3, and T reflex amplitude*

	RT	SCR	N100	P3	T reflex
Recovery	+	+	+	+	+
ISI x Recovery	–	0	–	+	–
Relevance x Recovery	0	+	–	+	–
ISI x Relevance x Recovery	0	0	+	–	–
Dishabituation	+	+	–	+ (Pz)	–
ISI x Dishabituation	–	0	+	–	–
Relevance x Dishabituation	0	–	–	–	–
ISI x Relevance x Dishabituation	0	0	–	–	+

Note: + significant; – not significant; 0 not tested

Recovery and dishabituation

Reaction time. As illustrated in Figure 5.4 and Table 5.2, reaction time to the deviant stimulus was longer compared to the last habituation stimulus, $F(1,26) = 30.59$, $p < .001$. This effect was independent of ISI.

Reaction time was longer to the renewed presentation of the habituation stimulus compared to the last standard, $F(1,26) = 5.96$, $p < .05$. This effect was also independent of ISI.

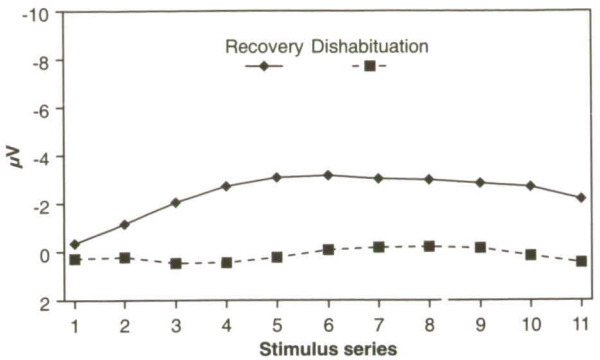

Figure 5.14. Difference between N100 amplitude (at Cz) to the deviant and predeviant stimuli (recovery), and difference between N100 amplitude to the postdeviant and predeviant stimuli (dishabituation) across stimulus series (ISI and stimulus relevance levels pooled).

SCR. Significant recovery of the SCR was found, $F(1,26) = 42.34, p < .001$. Figure 5.4 shows that Stimulus Relevance significantly influenced the magnitude of recovery, $F(1,26) = 5.90, p < .05$. Simple effect tests indicated a stronger recovery in the stimulus-relevant condition, $F(1,13) = 42.54, p < .001$, compared to the stimulus-irrelevant condition, $F(1,13) = 7.83, p < .05$.

The SCR dishabituated to the renewed presentation of the habituation stimulus $F(1,26) = 13.00, p < .05$. This effect was independent of Stimulus Relevance.

N100. There was a significant overall recovery effect, $F(1,52) = 13.56, p < .01$. Nevertheless, recovery of the N100 depended on specific combinations of Stimulus Relevance and ISI, $F(1,52) = 6.13, p < .05$. Only in the short-ISI/stimulus-relevant condition, $F(1,52) = 7.43, p < .05$, and in the long-ISI/stimulus-irrelevant condition, $F(1,52) = 11.83, p < .01$, recovery was significant. Recovery differed also between electrode positions, $F(8,45) = 2.27, p < .05$. No recovery was found at the frontal leads, whereas recovery was significant at the other leads (F ratios varied between 10.56 and 24.61).

N100 amplitude did not show a significant overall dishabituation effect. Dishabituation was affected by ISI, $F(1,52) = 7.01\ p < .01$, but not by Stimulus Relevance. Simple effect tests revealed a significant dishabituation only in the long-ISI condition, $F(1,26) = 7.03, p < .05$.

The next analyses pertained to the decrement of recovery and dishabituation of the N100 across the eleven blocks. As illustrated in Figure 5.14, both recovery and dishabituation of the N100 did not show decrement across the stimulation blocks.

P3. The deviant stimulus induced recovery of the P3, $F(1,52) = 140.38, p < .001$. P3 amplitude to the deviant stimulus was about the same magnitude as P3 amplitude

to the first stimulus (see Figure 5.10). Although recovery differed between electrode positions, $F(8,45) = 19.85$, $p < .001$, it was significant at all leads (F ratios varied between 32.68 and 173.93). Recovery of the P3 was influenced by ISI, $F(1,52) = 4.77$, $p < .05$, and Stimulus Relevance, $F(1,52) = 7.44$, $p < .01$. A more significant recovery was found in the short-ISI condition, $F(1,26) = 84.62$, $p < .001$, than in the long-ISI condition, $F(1,52) = 55.82$, $p < .001$. A more significant recovery was found in the stimulus-relevant condition, $F(1,26) = 123.71$, $p < .001$, than in the stimulus-irrelevant condition, $F(1,26) = 36.44$, $p < .001$.

The P3 failed to show a significant overall dishabituation effect. However, dishabituation differed across electrode positions, $F(1,52) = 2.93$, $p < .05$. Only at Pz, the P3 dishabituated significantly, $F(1,52) = 4.77$, $p < .05$. Dishabituation of the P3 at Pz was not influenced by ISI or Stimulus Relevance.

T reflex. The deviant tone elicited recovery of T reflex amplitude, $F(1,52) = 26.38$, $p < .001$, that was independent of ISI and Stimulus Relevance.

T reflex amplitude did not show a significant overall dishabituation to the renewed presentation of the habituation stimulus. Yet, dishabituation depended on a specific combination of ISI and Stimulus Relevance, $F(1,52) = 8.19$, $p < .01$. Simple effect tests revealed that only in the short-ISI/stimulus-relevant condition, dishabituation was significant, $F(1,13) = 4.06$, $p < .05$.

5.5 Discussion

Before discussing the results, a remark should be made about the failure to score SCR amplitudes in the short-ISI condition. As noted earlier, it was impossible to score the maximum skin conductance belonging to a particular trial because of the extent of overlap between individual responses. Others studying the SCR-OR and using a short ISI were, however, successful in scoring SCR (Bahramali et al., 1997; Barry et al., 1993; Lim et al., 1997; Williams et al., 2000). Bahramali et al. (1997) and Williams et al. (2000) used a more advanced technique developed by Lim et al. (1997) than employed in the current experiment to score maximum skin conductance. However, this technique also requires that different peaks in the skin conductance trace are to be discerned. In other words, our scoring technique does not explain the failure to score SCR amplitude. The major difference between the current study and the above-mentioned studies is the placement of the electrodes. The electrodes were placed under the foot whereas in the above mentioned studies the electrodes were placed on the volar surface of either the medial or distal phalanges of the second and third digits of the hand. We did not record SCR from the hand because in that case SCR might be confounded by the manual response that was required in the stimulus-relevant condition. It is conceivable that the characteristics of skin conductance differ for both recording sites leading to different results. In particular, under the foot, skin conductance might return to baseline at a slower rate.

5.5.1 Response decrement

As expected, SCR, N100, P3, and T reflex amplitude decreased curvilinearly with repetition of identical auditory stimuli. It may thus be concluded that the different response systems possess an important property of the OR, namely response decrement. We examined whether the decrement over trials of T reflex amplitude was similar to the decrement of the N100 and the SCR. As would be predicted by Näätänen and Picton (1987), T reflex amplitude decreased at the same rate as the N100, supporting the hypothesis that both response systems are functionally related. The decrement of T reflex amplitude differed significantly from the decrement of the SCR, probably because the response decrement between trials 1 and 2 was greater for the SCR than for T reflex amplitude. The decrement of the N100 was compared to decrement of the SCR and the P3 as well. Although the decrement of the N100 very much resembled the decrement of the SCR and the P3 (Figure 5.12) there were significant differences. In part, these might be ascribed to the specific statistical method (testing the linear and quadratic trends) being applied. In OR studies, several procedures have been used to test differences in the rate of response decrement. Each of them may yield different results (Boucsein, 1992; Siddle, Stephenson, & Spinks, 1983). It is conceivable that a different technique would produce other results than the technique used in the current experiment. We specifically refer to a technique in which the rate of response decrement is scored as the number of stimulus presentations necessary to reach a certain criterion, for example, two or three consecutive stimulus presentations which are smaller than some predetermined (and small) value. This index determines the end of the habituation process and is relatively unaffected by the initial difference in the rate of response decrement. So, whereas trend analysis revealed a difference in the rate of response decrement between, for example, the N100 and the P3 because response decrement between trials 1 and 2 was greater for the P3 than for the N100, the minimal amplitude criterion might not detect a difference because both ERPs decreased to the same response level. In short, we should be careful to interpret the results pertaining to the differences in the rate of response decrement. However, it is important to keep in mind that all recorded response measures rapidly decreased in a curvilinear fashion with repeated stimulus presentation.

We further examined the effect of ISI (short vs. long) and stimulus relevance (stimulus relevant vs. stimulus irrelevant) on absolute response magnitude and response decrement. In the current experiment, ISI and stimulus relevance produced mixed results in different response systems.

First, ISI and stimulus relevance differed in the effect they had on the *decrement* of SCR, N100, P3, and T reflex amplitude over identical trials. OR theory predicts that a longer ISI and a relevant stimulus are associated with a slower decrement than a shorter ISI and an irrelevant stimulus, respectively. The results showed that ISI only affected the decrement of the (ordinal) N100 and reaction time, that is, a slower decrement of the N100 and reaction time in the long-ISI condition than in the short-

ISI condition. Stimulus relevance had no influence on the trends in any response system.

Second, both experimental manipulations had a different effect on the *absolute magnitude* in different response systems. On basis of prior experimental findings and OR theory it was expected that in response to both a longer ISI and a relevant stimulus, absolute amplitudes of SCR, N100, P3, and T reflex would be enhanced in comparison to a shorter ISI and an irrelevant stimulus. ISI affected ERP amplitudes and reaction time (SCR could not be examined). N100 and P3 amplitudes were larger with long ISIs than with short ISIs. Reaction times were prolonged with long ISIs in comparison with short ISIs. Absolute T reflex amplitude was not affected by ISI. Stimulus relevance only had an effect on the ordinally averaged P3 amplitude, and on the N100 amplitude at Cz in the long-ISI condition. N100 and P3 amplitudes were larger in the stimulus-relevant condition than in the stimulus-irrelevant condition.

It may be questioned whether these results are in accordance with results of other habituation studies. The rate of response decrement of the N100 as well as the effect of ISI on N100 amplitude and its decrement were consistent with earlier results (see section 3.2.1). In previous studies on the habituation of the N100, the effect of stimulus relevance on the amplitude and on the decrement of the N100 has not been unequivocally established (see section 3.2.2). The current study also produced mixed results. Stimulus relevance did not influence the rate of decrement of the N100, whereas relevant stimuli elicited larger N100 amplitudes (at Cz) than irrelevant stimuli when the ISI was long. In section 3.2.2 it was already noted that the effect of stimulus relevance on N100 amplitude may depend on ISI. It was concluded that especially when ISI is variable, stimulus relevance affects N100 amplitude. This interaction effect may be caused by the increased time uncertainty introduced by the variability of the ISI. The fact that we found an effect of stimulus relevance on N100 amplitude with long ISIs but not with short ISIs is consistent with this hypothesis, because it might be reasoned that a long ISI induces a higher time uncertainty than a short ISI.

The fast rate of decrement of the P3 in the current study was also reported in several earlier studies, whereas others found a more delayed decrement of the P3 (see section 3.4.2). The rate of the decrement of the P3 will be further discussed in section 5.5.4. The observed effect of ISI on P3 amplitude, that is, larger P3 amplitudes with a long ISI than with a short ISI, was found earlier (e.g., Kenemans et al., 1989). As for the effect of ISI on the decrement of the P3, the results differ from those of Kenemans et al. (1989). In the current study, the P3 decreased equally fast in both ISI conditions, whereas in the study of Kenemans et al. the decrement of the visual P3 was faster in the short-ISI (2.45 s) condition than in the long-ISI (8.45 s) condition. The fact that stimulus relevance enhanced P3 amplitudes, but had no effect on the rate of response decrement is basically consistent with other habituation studies.

The curvilinear decrement of the SCR has been found in many habituation studies. Against the expectation, there was no effect of stimulus relevance on SCR amplitude and response decrement. Reviewing a number of studies on the effect of stimulus

relevance on SCR amplitude, Siddle et al. (1983) concluded that when stimulus significance is manipulated by requiring subjects to perform a reaction time task, SCR amplitude is augmented and its decrement is slowed. In the current study, N100 and P3 amplitude appeared to be more sensitive to manipulation of stimulus relevance than SCR amplitude.

5.5.2 Recovery and dishabituation

Recovery and dishabituation are important properties of the OR. Significant recovery and dishabituation would indicate that response decrement is caused by the loss of novelty and is not the result of a refractory state of the response system. Recovery was found for reaction time, SCR, P3, and T reflex amplitude. Recovery of the N100 was only significant when both ISI was short and the stimulus was relevant, and when both ISI was long and the stimulus was irrelevant. Recovery of the SCR and the P3 was enhanced by stimulus relevance as predicted by OR theory.

Dishabituation in response to the reappearance of the habituation stimulus was found for reaction time, SCR, and P3. The N100 showed dishabituation only with long ISIs, whereas T reflex amplitude dishabituated only in one out of four conditions (short-ISI/stimulus-relevant condition).

In summary, both reaction time, SCR, and the P3 fulfilled the three major defining characteristics of the OR, that is, fast response decrement, recovery, and dishabituation. T reflex amplitude showed response decrement and recovery. Recovery of the N100, and dishabituation of the N100 and T reflex amplitude depended on ISI and/or stimulus relevance.

5.5.3 Is there evidence for habituation of the N100?

A second objective of our study was to gain more insight in the habituation of the N100. Is the decrement of the auditory N100 the result of the loss of novelty (habituation hypothesis) or the result of refractoriness of the neural generators of the N100 (refractoriness hypothesis)? A number of findings might either support or dismiss the habituation hypothesis. First, significant recovery and dishabituation of the N100 would support the habituation hypothesis, whereas failure to find recovery and dishabituation would support the refractoriness hypothesis. However, the absence of significant overall recovery and dishabituation might also originate from the habituation of recovery and of dishabituation across stimulation blocks, reducing the effect in the ordinal average. Finally, the morphology of the decrement of the N100 and covariation between the decrement of the N100 and the SCR might either indicate a process of habituation such as defined by OR theory or a process involving refractoriness. In short, we aimed at investigating (1) recovery, (2) dishabituation, (3) the habituation of recovery and of dishabituation, and (4) the morphology of the decrement of the N100.

First, as outlined above, recovery was found in only two conditions (short-ISI/stimulus-relevant and long-ISI/stimulus-irrelevant). It is unclear why just these specific combinations of ISI and stimulus relevance yielded recovery to the deviant stimulus. It

is feasible that in the other two conditions (short-ISI/stimulus-irrelevant, and long-ISI/stimulus-relevant) the stimulus change evoked no OR. However, this argument is refuted by the results. In the conditions that did not demonstrate recovery of N100, the deviant trial elicited a significant P3, indicating deviance detection. In other words, the deviant tone was reflected in some features of the ERP. Therefore, it seems unlikely that the lack of recovery of the N100 was caused by generalization of habituation.

Second, the results revealed a significant dishabituation of the N100 to the renewed presentation of the habituation stimulus, but only when ISI was long. This might suggest that dishabituation might only be found with longer ISIs. However, this argument is contradicted by the results of Budd et al. (1998) who found no dishabituation of the N100 when ISI was 10 s. Another possibility is that the time uncertainty of the occurrence of the deviant stimulus may have affected the elicitation of dishabituation. In the STA studies that did not find dishabituation of N100, the deviant stimulus was always presented at the same position in the stimulus series (e.g., Barry et al., 1992; Budd et al., 1998; Fruhstorfer, 1971). Megela and Teyler (1979), however, did find dishabituation of N1-P2 when the presentation of the deviant stimulus was varied over 5 ordinal positions, with an interstimulus interval ranging between 5 and 10 s. The current study reported dishabituation of the N100 under similar conditions, that is, a relatively long ISI and variation of the position of the deviant over stimulus blocks. The data collected so far suggest that the interaction between ISI and predictability of the occurrence of the deviant is an important factor in eliciting dishabituation of the N100.

Third, it was tested whether a possible recovery of the N100 showed decrement across stimulus series as found by Kenemans et al. (1989) using visual stimuli. Decrement of recovery of the N100 might weaken the recovery effect in the ordinal average. Decrement of recovery of the N100 would be expected to occur especially in those conditions that fail to demonstrate recovery in the ordinal average. However, no evidence was found for such a decrement. In addition, dishabituation of the N100 also did not decrease over stimulation blocks.

The fourth issue was the morphology of the decrement of the N100. It was reasoned that repetition of identical stimulus series might induce a faster rate of the decrement of the ordinally averaged N100 compared to the decrement of the single trial N100 in the first stimulus series. The decrement of the ordinally averaged N100 and the OPTA N100 in the first stimulus series were similar. Figures 5.9 and 5.12 demonstrate that even in the first stimulus series, the decrement of N100 amplitude was the fastest across the first two trials compared to the decrement across the ensuing trials. Although this morphology might suggest refractoriness of the generators of the N100, the decrement is not very different from the decrement of SCR, supporting the habituation hypothesis.

In summary, the data of the "habituation" of the N100 tend to support the habituation hypothesis more than the refractoriness hypothesis. The first reason is that the

N100 decreased in a similar fashion as the SCR. The second positive finding was the dishabituation of the N100 in the long-ISI condition. Dishabituation is one of the crucial properties of the OR but has seldom been demonstrated for the N100. We hypothesize that dishabituation of the N100 depends on the time uncertainty of the occurrence of the deviant stimulus. A potential threat for the habituation hypothesis is that recovery of the N100 could not be demonstrated in all conditions. If the N100 is to be considered a cerebral index of orienting, the absence of recovery in half of the conditions is inconsistent with OR theories of habituation. However, the absence of recovery is also inconsistent with the refractoriness theory, claiming recovery of the N100 to be the result of activation of different neural populations by the habituation stimulus and the deviant stimulus (Näätänen et al., 1988). It would predict recovery of the N100 in every condition of the current experiment because of activation of fresh elements. The lack of recovery could not be explained in terms of habituation of recovery of the N100 across stimulation blocks. In this respect, our results contradict those of Kenemans et al. (1989) who demonstrated that recovery of the visual N100 decreased with repeated stimulus change.

5.5.4 The rate of the decrement of the P3

Of all response measures, the P3 was the most sensitive to the experimental manipulations because it showed fast response decrement, recovery, dishabituation, and was affected by ISI and stimulus relevance. Thus, in the current study the P3 may be considered a full-fledged cerebral OR component.

As noted above, a robust finding of this study was the very fast decrement over trials of the P3. Although fast decrement of the P3 was found earlier in several stimulus modalities (*auditory:* Bourbon et al., 1987; Megela & Tyler, 1979; Ritter et al., 1968, *visual:* Megela & Tyler, 1979, *somatosensory:* Kekoni et al., 1997), Verbaten et al. (1986a) and Kenemans et al. (1989) showed that the visual P3 decreased at a much slower rate than the vertex N100. There may be two alternative explanations for the dissociation between studies showing a fast decrement of the P3 and studies showing a slower decrement in comparison with the N100. First, a very fast decrement of P3 was found in studies using ordinal averages, whereas Verbaten et al. (1986a) and Kenemans et al. (1989) presented just one stimulus series using single trial estimates of the ERP. It might be reasoned that the method of ordinal averaging of identical stimulus blocks results in a speeded decrement of P3 amplitude because of two different processes. First, because identical stimulus blocks are repeatedly presented, the stimulus gradually looses its novelty. Second, the first stimulus in a stimulus block evokes a large P3 because of a high time uncertainty induced by the relatively long interblock interval compared to the ISI. As a result of these two processes, the large P3 elicited by the first stimulus might be greatly reduced in response to the second stimulus. In a STA study, Bruin et al. (2000) avoided this problem by presenting blocks of visual stimuli, each of them containing a qualitative different stimulus. Nevertheless, also in that study the ordinal

averages indicated a slower decrement of the P3 than of the N100, invalidating the idea that the ordinal averaging method would be responsible for the fast decrement of the P3. Our data also point against the notion that the fast decrement of the P3 is a perverse effect of the STA technique because the single trial P3, evoked in the first stimulus series, decreased in a similar fashion as the ordinally averaged P3. The decrement of both the P3 and the N100 is largest between the first and the second stimulation trial.

The second explanation of the differences in the rate of the decrement of the P3 concerns the type of stimuli being employed. Studies finding a very fast decrement of the P3 used simple auditory and visual stimuli, whereas studies showing a relatively slow decrement of the P3 and a fast decrement of the N100 presented complex visual patterns (e.g., Bruin et al. 2000). Verbaten (1997) suggested that the vertex N100 is involved in a more crude type of stimulus processing than the P3. If the P3 reflects cognitive evaluation of the stimulus and capacity-limited processing, the slower decrement of the P3 to complex visual stimuli may indicate that central processing is maintained longer due to the novelty and complexity of these stimuli. The notion that stimulus complexity has an effect on P3 amplitude is corroborated by Verbaten et al. (1986a) who manipulated the information conveyed by visual stimuli. Very complex stimuli elicited a larger P3 than less complex stimuli, whereas the N100 was unaffected by stimulus complexity. According to Verbaten (1997), the neuronal model underlying the N100 probably has a more limited number of parameters than the cognitive processes underlying the P3. The fact that in the current experiment the decrement of the P3 was relatively fast with repetition of identical simple auditory stimuli, is consistent with this hypothesis. The neuronal model of simple auditory stimuli may contain fewer parameters than the neuronal model of complex visual stimuli. Therefore, the central processing, as reflected by the P3, may be restricted to the first few stimuli.

5.5.5 The relationship between the N100 and audiospinal facilitation

A major objective of present study was to investigate a possible relationship between the (nonspecific) auditory N100 and T reflex amplitude. Näätänen and Picton (1987) hypothesized that audiospinal facilitation and the auditory N100 are functionally related and share a common generator. The generators of the nonspecific auditory N100 were said to belong to an extensive cerebral mechanism that functions to produce a widespread transient arousal facilitating sensory and motor responses to the eliciting stimulus. Specifically, the nonspecific N100 is the cortical projection of a reticular process that would also facilitate motor activity as reflected by the increase in spinal excitability. Parallel habituation of the N100 and T reflex amplitude would support this hypothesis and strengthen the notion that the N100 and audiospinal facilitation share a common generator. As expected, the current study found parallel decrement of the N100 and T reflex amplitude. However, the results on recovery and dishabituation suggest that the N100 and T reflex facilitation were more dissociated. Recovery and dishabituation of the N100 occurred partly in other conditions than recovery and dis-

habituation of the T reflex amplitude. The latter results indicate that the mechanism underlying the habituation of the N100 may be different from that of audiospinal facilitation.

Can the short-latency, audiogenic facilitation of T reflex amplitude be considered as an integral part of the OR? In the current study, it was demonstrated that T reflex facilitation possesses important criterion characteristics of the OR, namely response decrement and recovery. However, what is exactly the functional significance of this facilitation? Some authors (e.g., Liegeois-Chauvel, 1989) consider the increase in spinal excitability as a measurable physiological substrate of the startle reflex. Brunia and colleagues (e.g., Brunia & Boelhouwer, 1988) suggest that it is a reflection of a process alerting the whole motor system to be ready for action. Following the logic of the latter interpretation, it may be supposed that audiospinal facilitation induced by stimulus novelty should last longer than 100–200 ms after stimulus onset to be functional in facilitating adequate motor responses to the stimulus. Efficient adaptation to unexpected changes in environmental stimuli, bringing about considerable uncertainty about adequate responses to be undertaken, is most probably initiated later than 100 ms after stimulus onset. Therefore, if stimulus novelty causes the motor system to be brought closer to the motor action limit, generalized facilitation of the motor system should be prolonged for several hundred milliseconds. Therefore, two additional experiments were carried out to identify longer latency changes in spinal excitability induced by OR-evoking stimuli.

5.6 EXPERIMENT 3

Experiments 3 and 4 were conducted to study changes in the T reflex amplitude to infrequently presented auditory deviants (change in pitch) interspersed in a homogenous sequence of tones (standards). Such a deviation elicits a brain potential commonly known as the mismatch negativity (MMN) irrespective of the direction of the subject's attention for the stimuli (attend vs. ignore, Näätänen, 1992). The MMN is a negative brain potential peaking at about 150–250 ms after stimulus onset and has a frontal maximum. It reflects the outcome of a preattentive comparison process between the neural activity elicited by the incoming deviant and the neural representation of the standard (Näätänen, 1992). When stimulus presentations are attended to, a P3 potential is elicited next to a MMN. The P3 is a positive wave peaking at about 300 ms after stimulus onset and has a parietal maximum. The P3 is the manifestation of a mechanism that updates a model of the environment or context in working memory (Donchin, 1981; Donchin & Coles, 1988; Spencer, Dien, & Donchin, 2001). As discussed in chapter 3, the MMN and the P3 may be considered cerebral indices of – or are at least associated with – the OR, because both ERP components are evoked by stimulus deviation. The MMN reflects a call for central processing capacity, whereas the P3 can be regarded as a reflection of attention switching itself (Escera et al., 2000). In Experiments 3 and 4, we studied whether the occurrence of the MMN and the P3 to

deviant stimuli would be paralleled by enhanced T reflex amplitudes. In both experiments, there were two conditions. In the attend condition, aimed at evoking a P3, participants had to count the deviant tones that were of a higher pitch than the standard tones. In the ignore condition, aimed at evoking only a MMN, participants were reading a book and were instructed to ignore the auditory stimulation.

The main objective was to study the effect of stimulus deviance on T reflex amplitude when T reflexes were evoked at longer intervals following stimulus onset. In Experiment 2, the effect of a deviant tone on T reflex amplitude was significant when T reflexes were elicited at 100 ms after stimulus onset. A relevant question is whether this facilitation is prolonged at longer intervals. The reason to evoke T reflexes at longer intervals is that audiospinal facilitation induced by stimulus novelty should last longer than 100 ms after stimulus onset to be functional in facilitating adequate motor responses given the minimal response latency of such responses. Therefore, in Experiments 3 and 4, T reflex evocation was not limited to 100 ms after stimulus onset. In Experiment 3, the intervals between tone onset and T reflex evocation were 100, 200, and 300 ms, and in Experiment 4 the intervals were 200, 300, 400, and 500 ms. This procedure allowed us to examine the time course of T reflex facilitation elicited by a change in auditory stimulation.

5.6.1 Method

Participants

Twenty-four volunteers (22 women, 2 men) participated in this experiment. Their age ranged from 18 to 25 years (mean age was 19.9 years). The participants received course credits. No one reported hearing or vision disorders.

Procedure

Stimuli were standard pure tones (1000 Hz) interspersed with deviant tones (1100 Hz). Stimulus order was pseudorandomized with the standards occurring in 90% of the trials and the deviants in 10% of the trials. There was at least one standard between two deviants. Both standard and deviant tones had an intensity of 70 dB and a duration of 70 ms with 12 ms rise and fall times. Tones were produced by means of a 16 bit soundcard and were binaurally delivered through insertion headphones (Etymotics ER-2). Length of ISI was 2 s.

Two experimental variables were varied orthogonally, that is, attention and tone-reflex interval. Participants were subjected to either the attend or ignore condition. The two groups were of equal size. In the attend condition, participants were instructed to count the occurrence of deviant tones. In the ignore condition participants read a book of their own choice and were instructed not to respond in any way to the auditory stimuli. Tone-reflex intervals were 100, 200, and 300 ms, and were varied within participants. Participants were presented three series of 550 tones, each with a different

tone-reflex interval. There was a 5 min rest period between subsequent stimulus series. The order of the series was counterbalanced over participants. Participants were not told that different tone-reflex intervals were employed.

Physiological recording and scoring

Before and after each oddball series, 25 T reflexes without a preceding tone were evoked at 2-s intervals. For each stimulus series, the average of the 50 reflexes served as baseline value (100%). During the oddball series, T reflexes were evoked after each tone. T reflex amplitudes during the stimulation trials were expressed as a percentage of the baseline value after which the baseline value was subtracted from the obtained value. In other words, T reflex amplitude was expressed as the *percent change* from baseline in the statistical analysis.

ERPs were recorded with Ag/AgCl electrodes from F3, Fz, F4, Cz, and Pz (according to the 10-20 system). EEG measurement and EOG artifact correction were identical to those in Experiment 2.

ERP records (from 200 ms before stimulus onset until 600 ms after stimulus onset) and T reflexes amplitudes were separately averaged for the deviant tones and the standard tones immediately preceding the deviant tones. ERPs to the standard tone were then subtracted from the ERPs to the deviant tone resulting in difference waveforms. In an a priori chosen time window of 125–225 ms following stimulus onset, the maximal negative amplitude was scored as the amplitude of the MMN. For the P3, the maximal positive amplitude was scored in a time window of 250–500 ms following stimulus onset.

Statistical analysis

MMN and P3 amplitude scores were entered into a MANOVA for repeated measures. It was tested whether the amplitudes significantly differed from zero. The design comprised the within-subjects variable Lead (F3, Fz, F4, Cz, and Pz) and the between-subjects variable Group (reading vs. counting) to examine the effect of attention. T reflex amplitudes were analyzed by comparing the amplitudes (percentage change from baseline amplitude) belonging the predeviant trial with the amplitudes belonging to the deviant trial. Analysis by means of MANOVA included the within-subjects variables Tone (standard vs. deviant) and Tone-reflex Interval (100, 200, and 300 ms), and the between-subjects variable Group (reading vs. counting). A significance level of 5% was adopted for all statistical tests. The effect of Tone on the MMN, the P3, and T reflex amplitude was analyzed using one-tailed tests because of a priori expectations of the effects of this variable. No directional predictions were formulated for the effect of Group on MMN and T reflex amplitude. P3 amplitude was expected to be larger in the counting condition than in the reading condition.

5.6.2 Results

MMN and P3

Figure 5.15 presents the difference waves for the reading and counting conditions. The deviant stimulus elicited a clear MMN, with a maximal amplitude at about 160 ms following stimulus onset. In the counting condition, the MMN was followed by a N2b that is best visible at the frontal leads (Figure 5.15). MMN amplitude significantly differed from zero, $F(1,22) = 156.76$, $p < .001$, and differed between electrode positions, $F(2,21) = 7.90$, $p < .01$. For both conditions the MMN was largest at F4 and smallest at Pz. MMN amplitude was larger in the counting condition than in the reading condition, $F(1,22) = 12.71$, $p < .01$. It is unlikely that this effect of attention on MMN amplitude could be caused by an overlap with the N2b because, as Figure 5.15 shows, the N2b starts after the a priori window in which the amplitude of the MMN was determined. Furthermore, the effect of attention on MMN amplitude was already observed from onset of the MMN.

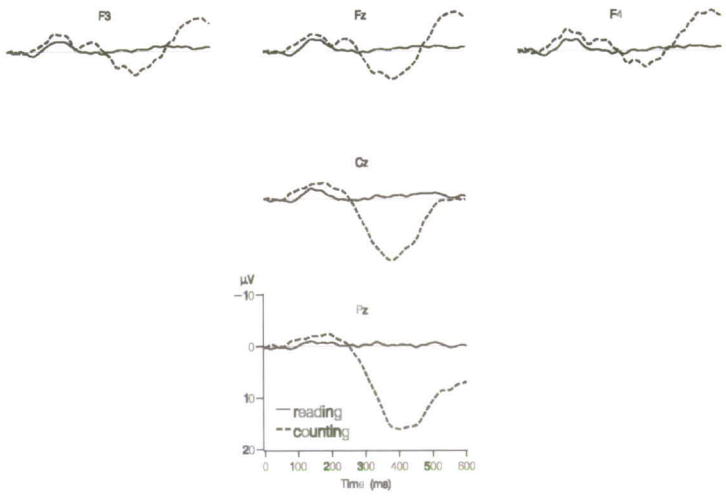

Figure 5.15. Grand average difference waves obtained by subtracting the ERP to the standard from the ERP to the deviant.

P3 amplitude was significantly larger than the prestimulus baseline level, $F(1,22) = 137.12$, $p < .001$. There was an effect of Group on P3 amplitude, $F(1,22) = 74.10$, $p < .001$. Figure 5.15 shows that in the counting condition, a P3 was elicited, $F(1,11) = 118.56$, $p < .001$, whereas in the reading condition, deviant tones did not evoke a significant P3. Only P3 amplitude in the reading condition varied with Lead, $F(4,8) = 26.56$, $p < .001$. The largest amplitude was found at Pz and the smallest at the frontal leads.

T reflexes

Overall T reflex amplitude was significantly enhanced by auditory stimulus presentation, $F(1,22) = 3.43, p < .05$ (Figure 5.16). This effect did not differ between groups. There was no effect of Tone-reflex Interval, nor a Tone-reflex Interval x Group interaction. T reflex amplitude to the deviant stimulus was larger than T reflex amplitude to the standard stimulus, $F(1,22) = 15.45, p < .001$. Tone did not interact with Group. Tone did, however, interact with Tone-reflex Interval, $F(2,21) = 5.53, p < .05$. Simple effect tests showed no difference in T reflex amplitude between the standard and deviant stimulus at a tone-reflex interval of 100 ms. At 200 ms and 300 ms, T reflex amplitude to the deviant stimulus was larger than to the standard stimulus, $F(1,22) = 3.24, p < .05$; $F(1,22) = 19.95, p < .001$, respectively. For both tone-reflex intervals, the effect of Tone did not interact with Group.

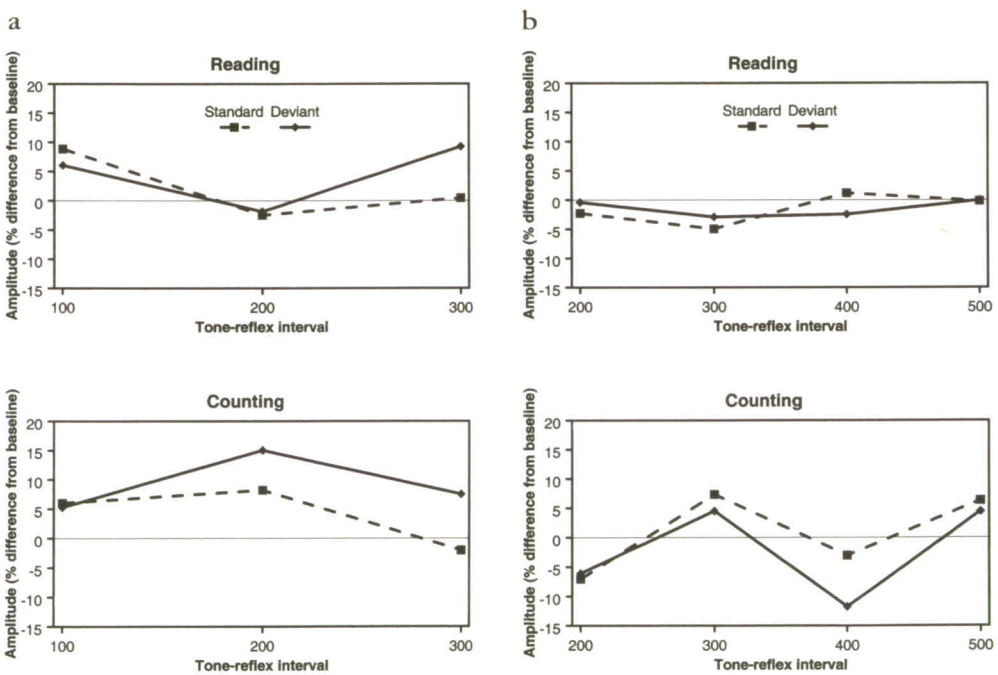

Figure 5.16. Mean T reflex amplitude to the deviant stimulus and the standard stimulus for Experiment 3 (a) and Experiment 4 (b).

Summarizing the results, stimulus change caused a relative increase in T reflex amplitude at 200 ms and 300 ms that was not significantly influenced by attention to stimulus presentation.

A major difference between the results of Experiments 2 and 3 concerns the effect of stimulus change on T reflex amplitude at a tone-reflex interval of 100 ms. In Experiment 2, T reflex amplitude showed recovery to a deviant stimulus, whereas in Experi-

ment 3, this effect was absent. A possible explanation for this discrepancy might be that the audiospinal facilitation elicited by deviant stimuli at 100 ms after stimulus onset was prone to habituation. In Experiment 2, there were only 11 deviant stimuli that were separated by intervals of at least 55 s. In Experiment 3, on the average 55 deviant stimuli were presented in each stimulus series, at a much shorter interdeviant interval. Because of the larger number of deviant stimuli and the shorter interdeviant intervals, it is feasible that T reflex facilitation at 100 ms elicited by deviant suffered from habituation with repetition of deviant stimuli. Therefore, a second analysis was carried out in which separately for both groups T reflex amplitudes at 100 ms to the first 10 standards (preceding the first 10 deviants) were compared to T reflex amplitudes at 100 ms to the first 10 deviants. This analysis revealed that in neither group T reflex amplitudes to the first 10 deviants were significantly different from T reflex amplitudes to the corresponding standard stimuli. This implies that even the first 10 deviants failed to elicit audiospinal facilitation measured at 100 ms after stimulus onset. This finding contradicts the results of Experiment 2.

5.7 EXPERIMENT 4

5.7.1 Method

Participants

Thirty-two volunteers (27 women, 5 men) participated in the experiment. Their age ranged from 18 to 35 years (mean age was 20.6 years). Participants received course credits or a monetary compensation. No one reported hearing or vision disorders.

Procedure

Experiment 4 was identical to Experiment 3 as far as stimulus parameters, task instructions, scoring, and statistical analysis were concerned. The only difference, apart from the fact that no EEG was recorded, was the interval between stimulus onset and T reflex elicitation (200, 300, 400, 500 ms).

5.7.2 Results

Overall T reflex amplitude was not facilitated by auditory stimulus presentation. There were no main effects of Group, Tone, and Tone-reflex Interval, and no significant Tone-reflex Interval x Group, Tone x Group, and Tone-reflex Interval x Tone x Group interactions. Although, the effect of Tone interacted with Tone-reflex Interval, $F(3,28) = 3.05$, $p < .05$, simple effect tests revealed no significant enhancement of T reflex amplitude as a result of stimulus deviation at any tone-reflex interval.

The results clearly contradicted those of Experiment 3. The facilitation of T reflex amplitude at 200 and 300 ms induced by stimulus deviance as found in Experiment 3, could not be replicated. The absence of any effect may be caused by the habituation of

audiospinal facilitation across the deviant tones. Therefore, a second analysis was carried out to test whether audiospinal facilitation at the different tone-reflex intervals elicited by deviant stimuli was significant for the first 10 deviant stimuli. For neither group or tone-reflex interval there was a significant effect of Tone. In other words, even the first 10 deviant tones did not enhance T reflex amplitude compared to T reflex amplitude to the preceding standard tones.

5.7.3 Discussion of Experiments 3 and 4

In Experiments 3 and 4 it was investigated whether qualitative changes in auditory stimulation enhanced T reflex amplitude at tone-reflex intervals ranging from 100 to 500 ms. Furthermore, it was tested whether attention for the deviant stimulus would influence this effect. The main research question was whether the recovery of T reflex amplitude at the 100-ms tone-reflex interval that was found in Experiment 2 could also be found at longer tone-reflex intervals. In Experiment 3, the shortest tone-reflex interval was 100 ms. Contrary to Experiment 2, T reflex amplitude evoked at this interval did not show recovery, not even to the first ten deviants, whereas in Experiment 3, at tone-reflex intervals of 200 ms and 300 ms stimulus deviance did induce significant facilitation of T reflex amplitude. Stimulus deviance may have had no effect on T reflex amplitude at 100 ms because the deviant tone in Experiment 3 (standard = 1000 Hz; deviant = 1100 Hz) did not differ as much from the standard as in Experiment 2 (standard = 1000 Hz; deviant = 500 Hz). The question then remains why it was enhanced at tone-reflex intervals of 200 ms and 300 ms. Although we found significant audiospinal facilitation at longer tone-reflex intervals induced by stimulus deviance, this is not a reliable finding and therefore probably an accidental effect, because in Experiment 4, which had more statistical power because of more participants (32 vs. 24), stimulus deviancy had no effect at all on T reflex amplitude at either of the four tone-reflex intervals (200, 300, 400, 500 ms).

The second factor that was studied in Experiments 3 and 4 was the attention for the auditory stimulation. Although the manipulation of attention was reflected in the brain potentials (P3), it had no effect on T reflex amplitudes. This finding is consistent with the results of Experiment 2 in which manipulation of attention also did not significantly affect T reflex amplitude. Thus, T reflex amplitude did not differentiate between automatic processing as indexed by the MMN and controlled processing as indexed by the P3.

5.8 General discussion

5.8.1 Is audiogenic facilitation of T reflex amplitude a motor component of the OR?

In this chapter the motor system was probed with T reflexes during the temporal course of the OR. It was questioned whether the short-latency enhancement of T reflex amplitude induced by auditory stimulation could be regarded as a motor index of the OR. It

was argued that the enhancement of T reflex amplitude during the OR may reflect the readiness for responding to unexpected novel changes in the environment. If this audiospinal facilitation is an integral part of the OR, T reflex amplitude should display the defining characteristics of the OR, including response decrement, recovery, and dishabituation. Four experiments were carried out using paradigms that produced in previous studies reliable cerebral and autonomic indices of the OR. The first two experiments focused on the habituation of T reflexes evoked at 100 ms after tone onset. It was found that T reflex amplitude decreased across the presentation of a series of identical stimuli at about the same rate as the N100 and SCR. Furthermore, habituated T reflex amplitude recovered to a stimulus of higher intensity and to a change in pitch. Dishabituation of T reflex amplitude was found after both an intensity increase and decrease, but not unequivocally after a pitch change, whereas the SCR-OR did show dishabituation in that situation. Contrary to the prediction of the OR theory, T reflex amplitude and its decrement across identical stimuli were not influenced by stimulus relevance. However, this also applied to the SCR-OR. Experiments 3 and 4 (oddball experiments) examined the changes in T reflex amplitude at prolonged tone-reflex intervals (100, 200, 300, 400, 500 ms) induced by deviations in auditory stimulus presentations. Stimulus deviance enhanced T reflex amplitude only at tone-reflex intervals of 200 ms and 300 ms in Experiment 3. In Experiment 4, stimulus deviance had no effect at all on T reflex amplitude. In neither oddball experiment, stimulus relevance had any significant effect on T reflex amplitude. The oddball experiments did thus not provide unequivocal evidence for facilitation of T reflex amplitude induced by an infrequent deviant stimulus. In part, this may be explained by the small difference between the standard and the deviant tone relative to Experiment 1. It might be that only a very salient deviant and/or an intensity increase provoke recovery of audiospinal facilitation.

The results of these experiments raise a number of questions. First, to what stimulus features does the T reflex, evoked after auditory stimulus presentation, respond? Does it respond to the novelty of the stimulus or to stimulus presentation per se, more specifically, the change in the level of energy impinging on the sensory receptors? Second, what is the function the short-latency audiogenic facilitation of spinal reflexes? Does it reflect an increase in the readiness for activity in the skeletal muscles as suggested by Brunia and Boelhouwer (1988), or is it a manifestation of a different response?

Based on the experimental results of this study and previous studies on EMG responses to auditory stimuli, the short-latency facilitation of T reflex amplitude seems to be more analogous to a startle reflex than to facilitation of involuntary evoked motor activity associated with orienting.

The first reason for this argument is that the stimulus characteristics causing reliable facilitation of spinal reflexes, in terms of intensity and rise time, correspond with the stimulus characteristics evoking a startle response. In spinal reflex studies, auditory stimuli usually have relatively high intensities of about 80–85 dB (e.g., Brunia et al., 1982; Liegeois-Chauvel et al., 1989; Rudell & Eberle, 1985; Scheirs & Brunia, 1985),

but also in the range of 90–110 dB (e.g., Beale, 1971; Delwaide, Pepin, & Maertens de Noordhout, 1993; Delwaide & Schepens, 1995; Rossignol, 1975; Rossignol & Melvill Jones, 1976) with very short or no rise/fall times. We are not aware of any reflex studies employing weak auditory intensities and/or long rise/fall times. Whereas weak auditory stimuli (in the range of 20–30 dB) evoke significant SCR-ORs (e.g., Barry & Furedy, 1993), it remains to be the question whether spinal reflexes are facilitated at these low intensity levels. In the current study, the stimulus characteristics in Experiments 2, 3, and 4 corresponded with the stimulus characteristics usually employed in OR studies, namely a moderate intensity (70 dB) and rise/fall times of 10–12 ms. However, even with these stimulus characteristics, stimuli may evoke cardiac startle, at least to the first stimulus presentations in a sequence. Data of Turpin and Siddle (1983) suggest that a 30-ms rise time, even for a 60-dB stimulus, was insufficient to prevent startle occurring in some subjects (30% of the subjects showed an accelerative heart rate component and 50% showed a decelerative component). In addition, the occurrence of an accelerative heart rate component may be concealed by a superimposed, predominant decelerative component so that the frequency of accelerative components is underestimated. Turpin, Schaefer, and Boucsein (1999) presented auditory stimuli (white noise; intensity 60 or 100 dB; rise time 5 or 200 ms) requiring no attention or response. They demonstrated the presence of accelerative and decelerative heart rate response components to 60-dB tones suggesting the occurrence of both startle and orienting responses. As rise time was shortened from 200 to 5 ms, there was a significant shift from orienting to startle responses, resulting in (1) larger electrodermal responses, (2) a shift toward heart rate acceleration, and (3) an overall increase in the frequency of bodily motor responses. Their data suggest that a strict boundary between orienting and startle responses does not exist. The experiments of Turpin and colleagues suggest that with the stimulus parameters used in our experiments, the auditory stimuli may have elicited cardiac startle along with somatic startle as manifested in enhanced T reflexes in Experiments 1 and 2. In Experiments 3 and 4, auditory stimulus presentation evoked little or no facilitation of T reflex amplitude. It is possible that in these experiments only the very first stimulus presentations evoked audiospinal facilitation. Because of the large number of stimulus presentations, facilitation of T reflex amplitude might have been lost in the average.

A second argument for not considering spinal reflex facilitation as a motor index of orienting, is that it is most probably not evoked by visual simulation. If facilitation of spinal reflexes is part of an orienting process with the function of facilitating response execution, it should also emerge with visual stimulation. The effect of visual stimulation on spinal reflexes was studied by Scheirs and Brunia (1982). They investigated whether in a warned reaction time paradigm, auditory or visual warning stimuli had a facilitory effect on T reflexes. T reflexes were evoked at tone-reflex intervals varying from 0 ms to 350 ms (in steps of 50 ms) after the onset of the warning stimulus. The results showed that the enhancement of T reflex amplitudes developed more slowly after visual than after auditory warning stimuli with an intensity of 85 dB. The enhance-

ment of T reflexes to visual stimuli did not show a maximum at 100 ms that is typical for auditory stimuli. The question is whether this slowly developing increase of T reflex amplitudes was the result of a general arousal process induced by the visual warning stimulus or whether it was more related to motor preparation to the imperative stimulus. In our opinion, enhancement of the T reflex amplitudes was probably associated with motor preparation to the imperative stimulus. This can be argued on the basis of the results of another experimental manipulation in the study of Scheirs and Brunia (1982). They evoked T reflexes after presenting a relatively soft tone (65 dB) at the same tone-reflex intervals as in the visual stimulus condition. The soft auditory stimulus condition was subdivided into two conditions. Participants were instructed either to listen passively to the stimuli or to perform a response to the imperative stimulus that was presented 4 s after the auditory warning stimulus. Scheirs and Brunia did not find enhanced T reflex amplitudes to passively attended soft tones, whereas in the fore-warned reaction time task, T reflexes were enhanced in almost exactly the same way as in the visual stimulus condition. In other words, only when motor preparation to the imperative stimulus was to be expected, T reflex amplitude showed a gradual increase after visual and soft auditory stimulus presentations. This facilitation could thus not be interpreted as an effect related to the presentation of the warning stimulus per se. The gradual increase in T reflex amplitudes across increasing stimulus-reflex intervals was not the result of the increased signal value of the warning stimulus, but probably reflects an early preparatory process to the imperative stimulus.

If the increase in T reflex amplitudes to the visual and soft auditory warning stimuli in the study of Scheirs and Brunia was really induced by the signal value of the stimulus, one would expect enhancement of T reflex amplitudes following attended target stimuli in the current oddball experiments because these stimuli were given signal value by a priori task instructions. However, stimulus relevance had no significant effect on T reflex amplitude. When the short-latency audiogenic facilitation of T reflex amplitude is to be considered as a manifestation of startle (cf. Delwaide & Schepens, 1995), it is hardly surprising that the visual stimulus in the experiment of Scheirs and Brunia (1982) did not induce a short-latency reflex facilitation. Although there are virtually no studies on whole body startle induced by photic stimuli, the data collected so far suggest that photic startle is limited to just an eyeblink and even this response is relatively difficult to elicit and is small compared to acoustic startle (Burke & Hackley, 1997; Hackley & Boelhouwer, 1997; Hackley & Johnson, 1996; Van Boxtel, Boelhouwer, & Bos, 1998). In addition, photic startle responses are usually evoked by an intense light stimulus like a photo-flash. In the experiment of Scheirs and Brunia (1982), a relatively low intensity light source was employed (a LED display). It is unlikely that such a low-intensity stimulus would evoke a startle reflex. Nevertheless, if poststimulus enhancement of T reflex amplitude would reflect an intrinsic motor component of orienting, any stimulus in any modality would elicit a short-latency T reflex amplitude modulation.

The third argument in favor of considering the audiogenic enhancement of T reflexes as a startle response is the time course of the facilitation of T reflex amplitudes. Audiospinal facilitation is a short-lived response extending from 50 ms up to 200 ms and peaking at about 100 ms after stimulus onset. Both onset and duration of audiospinal reflex facilitation match the onset and duration of the startle response. Landis and Hunt (1939) demonstrated that startle starts with an eyeblink and ends in the muscles of the limbs. This rostro-caudal latency shift of the startle response was also found in EMG studies. Wilkins, Hallett, and Wess (1986) recorded the audiogenic startle response in several muscles. It was found that the onset latency of the EMG response increased in a rostro-caudal manner: orbicularis oculi: 30–40 ms, masseter and sternocleidomastoideus: 55–85 ms, biceps brachii: 85–100 ms, hamstrings and quadriceps: 100–125 ms, and tibialis anterior: 130–140 ms. A similar pattern of onset latencies was found by Brown et al. (1991), Chokroverty, Walzack, and Hening (1992), and Sachdev, Cheem, and Aniss (1997). In short, the startle response progresses downward across the body, reaching its maximal amplitude in the lower limbs at about the same time as the maximum intensity of audiospinal facilitation. This was demonstrated more directly by Delwaide and Schepens (1995) who found that the maximal facilitation of H reflex amplitude, measured in the soleus muscle, corresponded to the onset latency of the EMG startle response in the soleus muscle. The fact that audiogenic reflex facilitation has a short onset latency and is of short duration poses a problem for considering it as a motor component of the OR with the function of facilitating response execution. In the introduction of this chapter it was hypothesized that orienting to novel stimuli causes the motor system to be brought closer to the motor action limit facilitating adequate responding to such stimuli. However, audiospinal facilitation has waned before the subject comes into action. Note, for example, that the reaction times of Experiment 2 were considerable longer (more than 300 ms) than the duration of the audiospinal facilitation (normally up to 200 ms after stimulus onset). Therefore, in Experiments 3 and 4, it was examined whether audiospinal facilitation was prolonged by stimulus deviance. A positive finding would suggest that motor facilitation is functionally significant and thereby an integral part of the OR. Contrary to the expectation, no convincing evidence was found for prolonged facilitation of T reflex amplitude to stimulus deviance.

In addition to the possible explanations discussed earlier for the absence of the expected effect in the oddball experiments, an alternative explanation may be mentioned. The short simple auditory stimuli that were used may contain not enough intrinsic salience to evoke a generalized motor response. Increased activity in the motor system, with the function to facilitate adequate responses, might arise only in situations in which the stimulus is highly salient, has high signal or high arousal value. Accordingly, the threshold for eliciting a longer lasting facilitation of the motor system may be higher than for the SCR-OR and cerebral indices of the OR. Particularly, it is conceivable that only changes in the environment that are perceived as relevant for the organism prepare the motor system for action. However, our results are not in line with

the latter hypothesis because in none of the experiments, stimulus relevance had any significant effect on T reflex amplitude at any tone-reflex interval.

Habituation of T reflex amplitude is a crucial factor in the discussion of the status of audiospinal facilitation as a motor component of the OR. The observed fast decrement of T reflex amplitude to repetition of identical stimuli does not automatically imply that T reflex facilitation is an index of the OR because it is generally acknowledged that cardiac startle (Graham, 1979) and somatic startle responses rapidly decline with repeated presentation of startle-eliciting stimuli as well. Fast decrement of somatic startle responses – measured by surface EMG of several muscles – was repeatedly found (Brown et al., 1991; Chokroverty et al., 1992; Davis, 1948; Davis & Henninger, 1972; Gogan, 1979; Sachdev et al., 1997; Wilkins et al., 1986). Gogan (1970) studied habituation of EMG responses in facial, neck, and arm muscles to bursts of white noise with an intensity of either 32, 66, or 92 dB. He discerned two different responses, an early and a late one. The stability and constancy of these responses varied between muscles and depended on the position of the subject. The most stable responses were recorded from the orbicularis oculi muscle. The first response in the orbicularis oculi muscle had a latency of 20 to 40 ms and lasted about 160 ms, whereas the second response was prolonged, from 3 to 10 s. The early response showed a positive correlation with stimulus intensity, whereas the late response did not show such a relationship. The early response decreased more quickly with stimulus repetition than the late one. Gogan (1970) considered the early response to be the EMG recording of the startle reflex, while the late response was supposed to be related to orienting.

In summary, only transient auditory stimuli of relatively high intensity evoke elevated T reflex amplitudes. The short latency audiospinal facilitation is considered to be a manifestation of the startle response because their antecedent conditions, the time course, and the involved neural circuits are alike (Delwaide & Schepens, 1995; Liegeois-Chauvel et al., 1989). Auditory stimuli that are not intense enough to evoke a whole body startle, can nevertheless induce audiospinal facilitation. Thus, audiospinal facilitation is a highly sensitive index of the startle response. Although the startle reflex is largely determined by the physical stimulus characteristics, such as stimulus intensity and rise time (Graham, 1979), the current habituation experiments (especially Experiment 2) demonstrated that the audiogenic reflex facilitation is affected by the novelty of the stimulus as well. In these experiments, the influence of stimulus novelty is manifested in the fast habituation of T reflex amplitude when the same stimulus was repeatedly presented, and in the recovery to a (relative large) qualitative stimulus change, indicating the role of a mismatch with regard to recent stimuli.

The short-latency discharge or increase in excitability of motor neurons probably does not reflect a generalized motor preparation toward anticipated muscular activity. First, if audiospinal facilitation is an integral part of the startle response, the function of this response is perpendicular to the function of the OR. Whereas orienting involves attention directed toward the OR-eliciting stimulus and reflects stimulus intake, the

startle response represents an interruption of ongoing behavior and withdrawal from the stimulation. Second, the enhancement of motor activity lasts too short to facilitate response execution during the OR. Increased spinal excitability should be prolonged for several hundreds milliseconds, probably even several seconds, thereby covering the time needed to respond. However, Experiment 4 did not find evidence for a prolonged effect of (novel) stimuli on T reflex amplitude.

5.8.2 Additional evidence against the motor preparatory function of the OR

The current results did not provide converging evidence for the hypothesis that the OR facilitates motor output processes. Other studies also point against the motor facilitation hypothesis. Lynn (1966) advanced that there is evidence for the motor-facilitation function of the OR by arguing that visual reaction time is decreased when it is accompanied by an auditory, accessory stimulus. Facilitation of reaction time induced by presentation of two heteromodal stimuli separated by a short interval has been found in numerous studies (Spinks & Siddle, 1983). The question is whether this facilitation is an orienting effect. Alternative explanations have been proposed such as energy summation (Nickerson, 1973) or temporal cueing (Nickerson, 1965; Snodegrass, 1969). Intersensory facilitation might also be attributed to a brief surge of arousal, called automatic alerting (Hackley & Valle-Inclán, 1998). There is, however, controversy about which stage in the information processing is influenced by automatic alerting. Sanders (1980, 1983) suggested that automatic alerting affects the late motor adjustment stage, whereas Posner (1978) hypothesized the involvement of an earlier stage, the process of orienting to and then perceptually categorizing the reaction stimulus. Hackley and Valle-Inclán (1998) demonstrated that automatic alerting does not speed late motoric processes. In their experiment the lateralized readiness potential (LRP) was recorded in a Go-NoGo task with visual stimuli. The LRP reflects hand specific response preparation. In half of the trials the visual signal was preceded by an auditory, accessory stimulus at an interval of 30 ms. LRPs were averaged either stimulus-locked or response-locked. It was reasoned that if the accessory stimulus would facilitate a perceptual or decision-level process, the interval between stimulus and LRP onset would be shortened. In that case, no effect on the response locked LRP is to be expected. On the other hand, if alerting facilitates motoric processes, the interval between the onset of the response-locked LRP and the movement onset should be shortened. The response-locked LRPs for stimuli with and without the accessory stimulus were almost exactly identical, whereas the interval between the stimulus and LRP onset was shortened by the accessory stimulus. Even in the NoGo trials in which the late motor process was not engaged, a brief stimulus-locked LRP was speeded by the accessory stimulus. To conclude, the speeded responses due to an accessory stimulus, which would point to motor output facilitation during the OR according to Lynn, were not induced by facilitation of late motor processes. Hackley and Valle-Inclán (1998) hypothesized that either visual feature analysis, stimulus categorization, or response selection was facilitated.

An additional source of evidence against the motor facilitation hypothesis comes from studies in which the OR was probed with a concurrently performed reaction time task. If the OR has primarily a motor output-enhancing function, one would expect that motor performance is improved during the OR because the motor system is brought closer to the motor action limit resulting in faster responding. Shek and Spinks (1986) argued oppositely that if the OR induces sensory enhancement effects, it may lead at the same time to deterioration of motor performance because of the presumed antagonistic relationship between input and output systems (Routtenberg 1968, Graham, 1979). It is reasoned that motor responses deteriorate during an OR because the available processing capacity is redistributed between input and output processes with the emphasis on input processes. To test this hypothesis Shek and Spinks probed the OR with a concurrently performed reaction time task at 500 ms after the OR-eliciting stimulus. It was predicted that because of the presumed input-facilitation function of the OR, reaction time would be increased because additional time would be required to transfer the allocated processing capacity to the effector span. In line with their hypothesis, reaction time was slower during the presence than during the absence of a visual orienting stimulus. These findings were confirmed by Dawson, Filion, and Schell (1989), Filion, Dawson, and Schell (1994), and Niepel (2001) with auditory OR-evoking stimuli and visual reaction signals. In the studies of Dawson and colleagues, participants received intermixed presentations of to-be-attended and to-be-ignored tones. Visual probes were positioned at either 150, 300, 600, and 2000 ms after stimulus onset. The inhibition of reaction time was the strongest to the probe at 150 ms. Thus, the time at which the disruption of reaction time was maximal coincided with the time at which the intensity of audiospinal facilitation reaches its maximum.

Finally, reaction times in Experiment 2 of our study also contradicted the hypothesis of the OR favoring motor output. Activity in the motor system as indexed by T reflex facilitation was positively correlated with reaction time. When T reflex amplitude was facilitated to the first stimulus presentations and to the deviant tone, reaction time was slowed. Increased reaction time to initial stimulus presentations and to a stimulus change may reflect a process of resource reallocation aimed at input related processes.

In conclusion, our study and the studies discussed in this section do not support the notion that the OR facilitates the motor system with the ultimate goal of improving response execution. Instead, experimental findings presented so far suggest that the OR indicates the enhancement of perceptual processing as originally proposed by Sokolov (1960, 1963).

5.8.3 Methodological evaluation of T reflex evocation as a tool for studying motor manifestations of orienting

It may be questioned whether T reflexes are an adequate or effective tool for investigating motor manifestations of orienting. Despite the fact that evocation of T reflexes can result in a more sensitive measure of motor activity than surface EMG, there are,

however, some methodological drawbacks of this technique in studying the OR, which eventually prevent us from continuing using T reflexes in forthcoming experiments. The major problem is the poor time resolution due to the fact that per trial only one T reflex can be evoked. So, a detailed description of motor activity with a high time resolution over a longer period, for example 10 s, is virtually unattainable unless a large number of trials of different tone-reflex intervals (which is, however, impossible in habituation studies) or a large number of subjects are used, or both. In both instances, T reflex evocation is not an ideal method for studying motor manifestations during the temporal course of the OR because it does not elucidate within one trial the relevant changes of motor activity over time. Therefore, for the exploratory purposes of this study, a measure is required with a higher time resolution to investigate changes in motor activity, implying that surface EMG activity is a good candidate. In the end, the fact that T reflex evocation may result in a more sensitive measure of motor activity than surface EMG does not countervail the drawbacks of this technique.

Another issue that needs to be discussed is the level at which the motor system is probed by employing spinal reflexes as a tool. It may be questioned whether the primary locus of the motor effect of the OR is at the lumbar level of the spinal cord. Motor activity of other muscles may have a more functionally significant role during the OR. As concluded earlier, there is no indication that the OR facilitates response execution. On the contrary, the OR probably modifies the perceptual system for more efficient information processing. It may be questioned whether and where we can find motor manifestations of the OR that subserve this function of the OR, that is, increasing analyzer sensitivity. This question has still not been answered as Sokolov (1963, p. 13) already noted: "A serious defect in work done on the orientation reflex has been that its autonomic and motor manifestations have usually been studied quite apart from its most important function, the enhancement of analyzer sensitivity." In a comment on a paper of Barry (1990), Sokolov repeated his criticism. When the function of the OR is considered, changes in the activity of muscles should be studied that might have a functional role during stimulus intake. The next section argues that this role may be assigned to pericranial muscles.

5.8.4 Forthcoming experiments

In forthcoming experiments pericranial EMG activity will be recorded during the temporal course of the OR. The rationale for recording pericranial EMG activity is that several researchers presume a functional role of pericranial muscle activity during stimulus intake (e.g., Brunia, 1984). Specifically, Van Boxtel, Damen, and Brunia (1996) hypothesized that inhibition of masticatory and lower facial muscle activity enhances auditory sensitivity. In the next chapter, this hypothesis is tested. In chapter 7, it is investigated whether inhibitory pericranial EMG responses can be considered intrinsic components of the OR. Because of the presumed relationship between pericranial EMG activity and auditory sensitivity, we argue that during the OR, pericranial muscle activity will be inhibited to subserve the sensory-enhancing function of the OR.

Chapter 6

Inhibition of pericranial muscle activity, respiration, and heart rate enhances auditory sensitivity*

* Stekelenburg, J. J., & Van Boxtel, A. (2001). Inhibition of pericranial muscle activity, respiration, and heart rate enhances auditory sensitivity. *Psychophysiology, 38,* 629-641.

6.1 Abstract

We investigated whether previously observed inhibition of pericranial electromyographic (EMG) activity, respiration, and heart rate during sensory intake processes improves auditory sensitivity. Participants had to detect weak auditory stimuli. We found that EMG activity in masticatory and lower facial muscles, respiration, and heart rate were more strongly inhibited when stimulus intensity was gradually lowered to threshold level whereas EMG of upper facial muscles progressively increased. Detection of near-threshold stimuli was inversely related to prestimulus EMG levels in masticatory and lower facial muscles. In two additional experiments, it was investigated whether steady, voluntary contractions negatively influence auditory sensitivity. As expected, contraction of zygomaticus produced an increase in auditory threshold in comparison with contraction of corrugator or first dorsal interosseus. It is concluded that attention to external stimuli is accompanied by quieting of those somatic activities that produce internal noise or are accompanied by impaired middle ear transmission of auditory stimuli.

6.2 Introduction

Several 19th-century writings on expressive movements present observations on pericranial and respiratory actions that are triggered by unexpected auditory stimuli. Piderit (1858, p. 59) asserted that people who try to become aware of a weak auditory stimulus keep their mouth open to improve the sensation of the stimulus. Gratiolet (1865, pp. 232–234) claimed that there is a short suspension of breathing when the mouth is partly kept open during orienting to a sudden auditory stimulus. Voluntary muscle actions are stopped and also "the heart stops beating" during a surprising auditory sensation (pp. 256–257). Building on these observations, Darwin (1872, p. 283) concluded that an open mouth allows a more quiet breathing during the occurrence of a surprising, unexpected sound. He stated that it is easier to perceive the sound if breathing is quieted or stopped and the body is kept motionless. Helmholtz (1864/1883) had already observed that muscular contractions generate internal sounds at the lower limit of the audible frequency range. He found that such sounds were not only produced by the masticatory muscles but also by the much weaker facial and tongue muscles and the platysma.

These older observations suggest that breathing and other somatic activities are suppressed during the presentation of a weak or unexpected sound stimulus. Van Boxtel, Damen, and Brunia (1996) proposed a functional role of the activity of pericranial muscles in the detection of peripheral stimuli. They found a typical electromyographic (EMG) activity pattern during the anticipation of an auditory or visual imperative signal in a warned reaction time task: (a) a gradual EMG inhibition in masticatory muscles (temporalis, masseter, and mylohyoideus) and muscles in the lower part of the face (orbicularis oculi and zygomaticus major); and (b) a gradual increase of EMG in muscles in the upper part of the face (frontalis and corrugator supercilii). Although the

subjects were informed about the modality of the forthcoming reaction signal, the EMG responses were virtually independent of the sensory mode of the stimulus. At the same time, a heart rate deceleration was found that appeared to be related to the magnitude of the EMG responses. A stronger bradycardia was associated with a stronger EMG inhibition in the first group of muscles and a smaller facilitation in the second group. Slowing of the heart rate thus corresponded with smaller levels of spontaneous EMG activity in the two muscle groups.

Van Boxtel et al. (1996) hypothesized that the predominant pattern of pericranial inhibition is functionally significant by increasing the perceptual sensitivity for auditory and visual signals. With regard to auditory sensitivity, they proposed a direct and indirect effect. The direct effect implies a suppression of the internal sound vibrations that are generated by muscular contractions. These sounds are caused by the asynchronous, unfused twitch contractions of the active motor units (Orizio, 1993). The frequency spectrum of the soundmyogram generally shows a dominance of frequency components in the 0–100 Hz range. These frequencies are determined by the firing rates and the contractile properties of the active motor units. Although such sounds may be barely audible, it is possible that they are effectively transmitted to the inner ear via bone conduction and may constitute a background noise negatively affecting auditory sensitivity to external signals.

Indirect effects of pericranial muscular inhibition on auditory sensitivity may also exist. Various studies have found synkinetic covariations between activity of the middle ear muscles (stapedius and tensor tympani, innervated by the facial and trigeminal nerves, respectively) and voluntary activities like head movements, clenching the teeth, grimacing, laughing, yawning, coughing, swallowing, vocalization, and forcefully closing of the eyelids (Djupesland, 1965; Klockhoff, 1961; Salomon & Starr, 1963). Contractions of middle ear muscles induce increases in acoustic impedance (Burns, Harrison, Bulen, & Keefe, 1993; Jeter, 1976; Klockhoff & Anderson, 1960) and auditory thresholds, in particular for sound frequencies below 1000 Hz (Reger, 1960; Smith, 1943). We may thus hypothesize that pericranial relaxation is accompanied by relaxation of middle ear muscles, producing lower auditory thresholds for low-frequency sounds.

In addition to positive effects of pericranial muscular relaxation on auditory sensitivity, there may be positive effects on visual input. Inhibition of orbicularis oculi EMG activity may diminish interference with visual input by lowering the probability that endogenous eye blinks occur. The spontaneous EMG activity in orbicularis oculi observed by Van Boxtel et al. (1996) showed the same time course as the inhibition of eye blinks during the anticipation of a visual stimulus (Bauer, Goldstein, & Stern, 1987; Goldstein, Bauer, & Stern, 1992). The absence of clear effects of modality-specific attention on the pericranial EMG responses in the study of Van Boxtel et al. suggests the involvement of a centrally controlled motor response pattern that is directed to a nonspecific enhancement of the sensitivity of different sensory modalities. A parallel can be drawn with Sokolov's (1963) conception of the generalized orienting response as

a complex of efferent autonomic and somatomotor responses to external stimulation that is directed to a nonspecific increase in peripheral receptor sensitivity.

Van Boxtel and Waterink (1994) observed that the pattern of pericranial inhibition and facilitation in combination with bradycardia during stimulus anticipation was also correlated with a tendency to expiration. A few earlier studies tentatively reported an integrated pattern of pericranial EMG inhibition, bradycardia, and suppression of breathing or a tendency to expiration during anticipation of an aversive stimulus or a reaction signal (Obrist, 1968; Obrist, Webb, & Sutterer, 1969). In general, it is assumed that inhibition of heart rate, respiration, and bodily movements is characteristic of voluntary attention or involuntary orienting to external stimuli, in particular stimuli of low or moderate intensity (see, e.g., Graham, 1979; Sokolov, 1963; Turpin, Schaefer, & Boucsein, 1999). According to Sokolov (p. 166), the generalized orienting response is particularly manifest when stimulus intensity is near threshold level or when discrimination between stimuli is difficult. Later studies confirmed Sokolov's observations. It was found that nonsignal auditory stimuli elicited a larger instantaneous heart rate deceleration (Jackson, 1974) and a larger prolongation of the respiratory cycle (Poole, Goetzinger, & Rousey, 1966; Rousey & Reitz, 1967) the more stimulus intensity approached the auditory threshold intensity. In studies measuring heart rate during expectation of a significant stimulus, the heart rate deceleration response was larger when discrimination between the spatial properties of visual stimuli was more difficult (Coles, 1974; Gaillard & Perdok, 1979). A similar effect was found when subjects had to discriminate between the pitch of auditory reaction signals (Duncan-Johnson & Coles, 1974; Coles & Duncan-Johnson, 1977).

The current study was undertaken to investigate the hypothesized functional role of pericranial muscle responses with regard to the sensitivity to auditory signal or nonsignal stimuli. Three experiments were carried out. In the first experiment, pericranial EMG responses, heart rate, and respiration were measured during an auditory signal detection task. We expected that as signal intensity was lowered to threshold level, increasing the difficulty of detection, pericranial EMG activity would be proportionally inhibited in parallel with increasing bradycardia and suppression of respiration (i.e., suspension of inspiration and prolongation of the respiratory cycle) to raise the chance of detection. On the basis of the results of Van Boxtel et al. (1996), we expected EMG inhibition to occur widely spread in pericranial regions with the exception of the muscles in the upper part of the face (frontalis and corrugator) for which facilitation was expected.

As these expectations were confirmed, we investigated more closely the causal relationship between the observed pericranial EMG responses and stimulus detection rates. In two additional experiments, auditory threshold was assessed during steady, voluntary muscular contractions of varying strength that were maintained by means of visual EMG feedback. The effects of contractions of two representative pericranial muscles and a small hand muscle were investigated. The results supported the hypothesis that pericranial relaxation lowers the auditory threshold for low-frequency sounds.

6.3 EXPERIMENT 1

6.3.1 Method

Participants

Twenty healthy right-handed female and four male volunteers participated in the experiment. Ages ranged from 18 to 40 years with a mean of 22.2 years. The participants received course credits or a monetary compensation. Because of the placement of electrodes behind the ear for the measurement of EMG activity from the auricularis posterior muscle, only persons who were not wearing glasses were invited. In addition, only persons with normal hearing were admitted. No one reported hearing difficulties.

Experimental task and procedure

Participants were seated in a comfortable armchair in a sound-attenuated and electrically shielded chamber. Auditory stimuli were produced by means of a 16 bits soundcard and presented binaurally through circumaural headphones (Sennheiser HD 565). The stimuli were pure 1500-Hz tones of 4 s duration with linear rise and fall times of 100 ms. Stimulus onset asynchronies were equally distributed between 10 s and 55 s in steps of 5 s with a mean of 32.5 s. Before the start of the experiment, the participant's absolute hearing threshold for the 1500-Hz tones was established using a staircase procedure. Stimuli of six different intensities were used, adjusted to the participant's absolute hearing threshold: 0, 2, 4, 8, 24, and 48 dB(A) SL above threshold. Participants were instructed to listen carefully to the stimuli and to push a response button, held in the right hand, with minimal force when a stimulus was detected. To prevent confounding of pericranial muscle responses by motor preparation of the target response, it was emphasized that an unspeeded or delayed response had to be made after the tone had finished and that responses would just signal detection of a stimulus.

The experiment consisted of six stimulation trial blocks of 20 min duration that were separated by rest periods of 5 min. In each trial block, seven stimuli of each intensity level were presented in a random order, under the condition that two consecutive tones were of different intensities. This amounted to a total of 42 stimuli per intensity level.

Recording and scoring of physiological signals

Bipolar EMG activity was recorded from eight different pericranial muscles (frontalis, temporalis, corrugator supercilii, orbicularis oculi, zygomaticus major, orbicularis oris inferior, mylohyoideus, and auricularis posterior). See Figure 6.1 for the electrode placements. The temporalis muscle seems the most relevant masticatory muscle for the current study because it is specially involved in tonic jaw closing activity (Desmedt & Godaux, 1979). Opening of the mouth during the presentation of a weak or unexpected sound stimulus thus predominantly depends on inhibition of temporalis EMG activity. The auricularis posterior muscle was included in this study because of its vestigial

function analogous to pinna retraction in nonhuman species, presumed to attenuate the sensory impact of strong auditory stimuli. For locating the auricularis posterior muscle, the same procedure was followed as used by Hackley, Woldorff, and Hillyard (1987). The pinna was pulled outward and forward until a wedge-shaped protrusion behind the ear, corresponding to the tendon of insertion, was found. On each muscle, two Ag/AgCl surface electrodes with a contact area of 2 mm and casing of 11 mm diameter were placed in a direction parallel with the muscle fibers with 15 mm distance between electrode centers. The common reference electrode, which had a contact area of 8 mm diameter, was placed about 4–5 cm above the nasion. For half of the participants, EMG activity was recorded from the left side of the head, for the other half, EMG was recorded from the right side. EMG signals were high-pass filtered with a –3 dB cut-off frequency at 20 Hz (43 dB down/octave), low-pass filtered with a –3 dB cut-off frequency at 600 Hz (30 dB down/octave), and digitized (12 bits) at a rate of 1000 Hz. For each trial, 10-s EMG data records were stored: 4 s baseline immediately preceding stimulus onset, 4 s during stimulus presentation, and 2 s after stimulus offset. EMG data records during trials with detected stimuli were selected for further analysis. EMG signals were checked off-line for gross movement artifacts. Trials were rejected when across several muscles abnormally large bursts of spontaneous EMG activity occurred that lasted several seconds and started within 4 s before stimulus onset. EMG signals were full-wave rectified and mean rectified EMG amplitude was calculated for 0.5-s intervals resulting in 20 data points per trial. For each auditory stimulus intensity condition, EMG amplitude scores were averaged across valid trials. In the average data records, each data point was expressed as a percentage of the mean baseline EMG amplitude. Finally, the mean percentage score during the last 3 s of stimulus presentation minus the baseline level was calculated as a measure of the stimulus-related EMG amplitude response (inhibition or facilitation), thus avoiding early phasic EMG responses such as startle in the first second following stimulus onset.

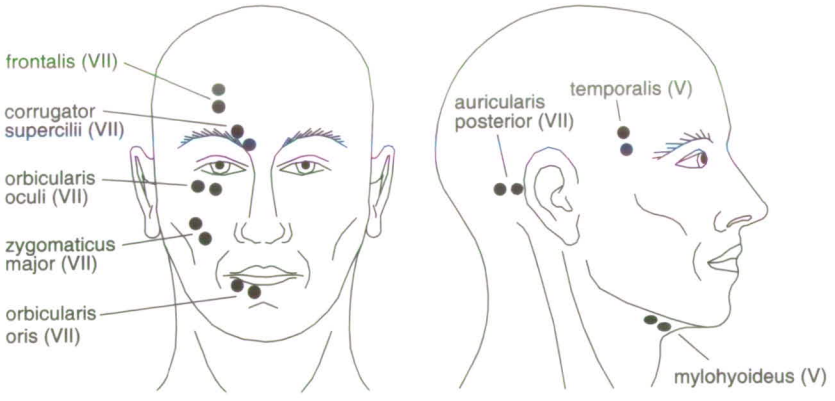

Figure 6.1. Placement of electrodes for surface EMG recordings. Roman numerals indicate muscular innervation by cranial muscles.

Respiration was measured by means of a respiration module that consisted of an elastic tube wrapped around the thorax just above the abdomen through which a 575-Hz tone was emitted by an oscillator that was attached to one end of the tube. Respiration caused variations in the length of the tube that were reflected by the phase difference of the tone between the oscillator and a sound-sensitive device connected to the other end of the tube. The phase difference was converted to a voltage that was digitized at a rate of 1000 Hz. For each trial, a data record was collected for a 10-s interval similar to that performed for EMG data (4 s baseline, 4 s stimulus presentation, 2 s poststimulus). Respiratory signals were averaged across the valid trials of the detected stimuli within a stimulus intensity condition. In the resulting mean respiratory signal, the mean baseline value was subtracted from each data point providing the stimulus-related respiratory response. As an amplitude measure of this response, the peak value (positive or negative) of the respiratory signal during stimulus presentation was determined.

The effect of auditory stimuli on respiratory period during stimulus presentation was also analyzed. For that purpose, inspiration and expiration time were added for each respiratory cycle during the 10-s data record. Inspiration time was defined as the interval between the start of inspiration and the moment of maximal inspiration. Expiration time was defined as the interval between maximal inspiration and the start of the next inspiration (cf. Wientjes, 1992). It was established whether stimulus onset occurred during the phase of inspiration (inspiratory trials) or expiration (expiratory trials). Respiratory period was determined separately for inspiratory and expiratory trials. For both types of trials, it was determined such that the respiratory cycle was considered to start with the respiratory phase during which the stimulus was presented (cf. Poole et al., 1966; Rousey & Reitz, 1967). This implied that for inspiratory trials, the respiratory cycle began at the start of the inspiration immediately preceding stimulus onset and ended at the start of the next inspiration. For expiratory trials, respiratory period was measured from the moment of maximal inspiration immediately preceding stimulus onset to the moment of the next maximal inspiration. To quantify the effect of stimulus presentation on respiratory period, the duration of the respiratory cycle including stimulus presentation was expressed as a percentage of the duration of the cycle immediately preceding stimulus onset. The obtained percentage scores were averaged across the valid trials of the detected stimuli within a stimulus intensity condition. To assess to what extent changes in respiratory period were caused by changes in inspiration or expiration time, this quantification procedure was also applied for inspiration and expiration time separately.

The electrocardiogram (ECG) was measured with Ag/AgCl electrodes with a contact area of 15 mm diameter that were placed on the sternum and the precordial position V6. The reference electrode was placed on the right scapula. The signal was relayed to a hardware R-wave detector (Mulder, 1988) that filtered the signal (–3 dB passband: 3.18–60 Hz), rectified it, and detected the R waves by triggering at the maximum slope of the ECG in the Q-R interval. The R-wave detector produced a 100-

ms square wave at each R wave that was digitized at a rate of 1000 Hz. R-wave event series were converted to interbeat intervals (IBIs). An artifact detection procedure was applied to search for prolonged IBIs due to missing R waves and short IBIs due to double triggering on both the R and T wave. A prolonged IBI was defined as an IBI that was longer than two times the mean IBI during the previous 10 s. A short IBI was defined as an IBI that was either shorter than 300 ms or shorter than 60% of the mean IBI during the previous 10 s. The correction procedure for prolonged IBIs consisted of splitting the prolonged IBI into two equal parts. When a short IBI was detected, it was added to the previous IBI. Following the procedure of Graham (1978), corrected IBIs were converted to heart rate (in beats per minute) during the same 20 intervals of 0.5 s as for which EMG and respiratory data records were collected (4 s baseline, 4 s stimulus presentation, 2 s poststimulus). The 20 data points were averaged across the valid trials of the detected stimuli within a stimulus intensity condition. The mean baseline value was subtracted from each data point to obtain the stimulus-related heart rate change. The peak value of this change (positive or negative) during the last 3 s of stimulus presentation was used as a measure of the magnitude of this response.

Statistical analysis

Using a multivariate analysis of variance (MANOVA) procedure for repeated measures, we tested whether percentage of detected stimuli and reaction time were related to stimulus intensity. For that purpose, the scores were transformed into linear and quadratic trend contrast scores across stimulus intensity by means of computation of orthogonal polynomials.

EMG amplitude, respiratory amplitude, respiratory period, and heart rate were subjected to analogous analyses to test whether auditory stimuli produced significant inhibition or facilitation. Using MANOVA for repeated measures, it was first tested whether the grand averages of EMG amplitude response (for each muscle separately), peak respiratory response, and peak heart rate change during stimulus presentation significantly deviated from zero. Similarly, the duration of the respiratory cycle containing stimulus onset was tested against the duration of the cycle immediately preceding stimulus onset. Second, we tested whether the physiological response scores were dependent on stimulus intensity by calculating linear and quadratic trend contrast scores.

A 5% significance level was adopted in all tests. On the basis of the results of Van Boxtel et al. (1996), a parallel inhibition was expected of respiration, heart rate, and EMG activity in temporalis, orbicularis oculi, zygomaticus, and mylohyoideus whereas EMG activity in frontalis and corrugator would be facilitated. Because of these directional predictions, difference contrast scores and linear trend contrasts associated with effects of auditory stimulation were subjected to one-tailed tests. Two-tailed tests were performed on contrast scores for EMG responses of orbicularis oris and auricularis posterior for which directional predictions were not formulated.

6.3.2 *Results*

Stimulus detection

Figure 6.2 presents mean percentages of detected stimuli and mean reaction times for the different stimulus intensity levels. Percentage of detected stimuli varied between 47.1% for stimuli of 0 dB and 99.8% for stimuli of 48 dB. It increased curvilinearly with stimulus intensity, as revealed by a significant positive linear trend, $F(1,23) = 284.76$, $p < .001$, and a negative quadratic trend, $F(1,23) = 394.23$, $p < .001$. The participants complied with the instruction to produce an unspeeded response as apparent from mean individual reaction times ranging between 4,750 and 7,321 ms across stimulus intensities ($M = 5{,}628.8$ ms). Mean reaction time decreased curvilinearly with stimulus intensity as apparent from a significant negative linear trend, $F(1,23) = 24.73$, $p < .001$, and a positive quadratic trend, $F(1,23) = 8.41$, $p < .01$.

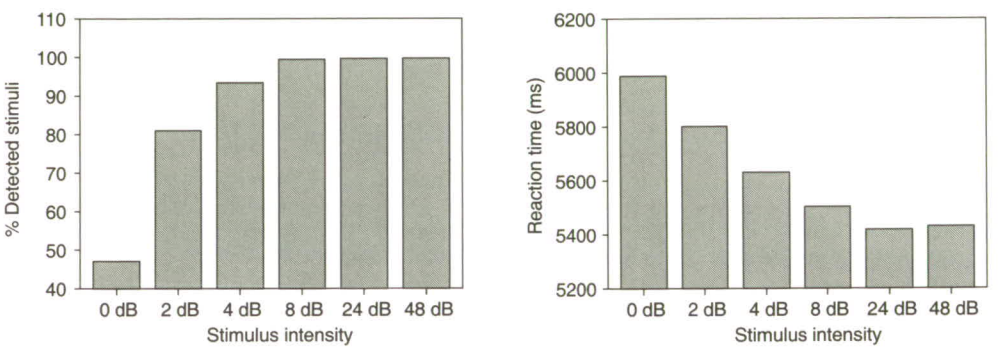

Figure 6.2. Mean percentage of detected stimuli and mean reaction time as a function of auditory stimulus intensity.

EMG amplitude

Figure 6.3 shows the mean EMG responses associated with the different stimulus intensity levels. Stimulus intensity differentially affected EMG activity of pericranial muscles. Visual inspection of Figure 6.3 suggests that for the majority of muscles (temporalis, orbicularis oculi, zygomaticus, orbicularis oris, mylohyoideus, and auricularis posterior), EMG amplitude decreased with decreasing stimulus intensity whereas for frontalis and corrugator, EMG amplitude increased.

We first present the results of the muscles for which EMG inhibition during stimulus presentation was a priori expected (temporalis, orbicularis oculi, zygomaticus, and mylohyoideus). First, we tested whether overall mean EMG activity during the last 3 s of stimulus presentation significantly differed from baseline. Significant inhibition was only found for orbicularis oculi, $F(1,23) = 26.07$, $p < .001$. Second, linear and quadratic trends of EMG amplitude across the different stimulus intensity levels were

investigated. In each of the four muscles, EMG amplitude was lower at weaker than at higher stimulus intensities. Curvilinear relationships were revealed by significant linear and quadratic trends (temporalis, linear $F(1,23) = 7.59$, $p < .01$, quadratic $F(1,23) = 5.01$, $p < .05$; orbicularis oculi, linear $F(1,23) = 9.21$, $p < .01$, quadratic $F(1,23) = 4.88$, $p < .05$; zygomaticus, linear $F(1,23) = 20.50$, $p < .001$, quadratic $F(1,23) = 11.13$, $p < .01$; mylohyoideus, linear $F(1,23) = 13.53$, $p < .001$, quadratic $F(1,23) = 9.33$, $p < .01$).

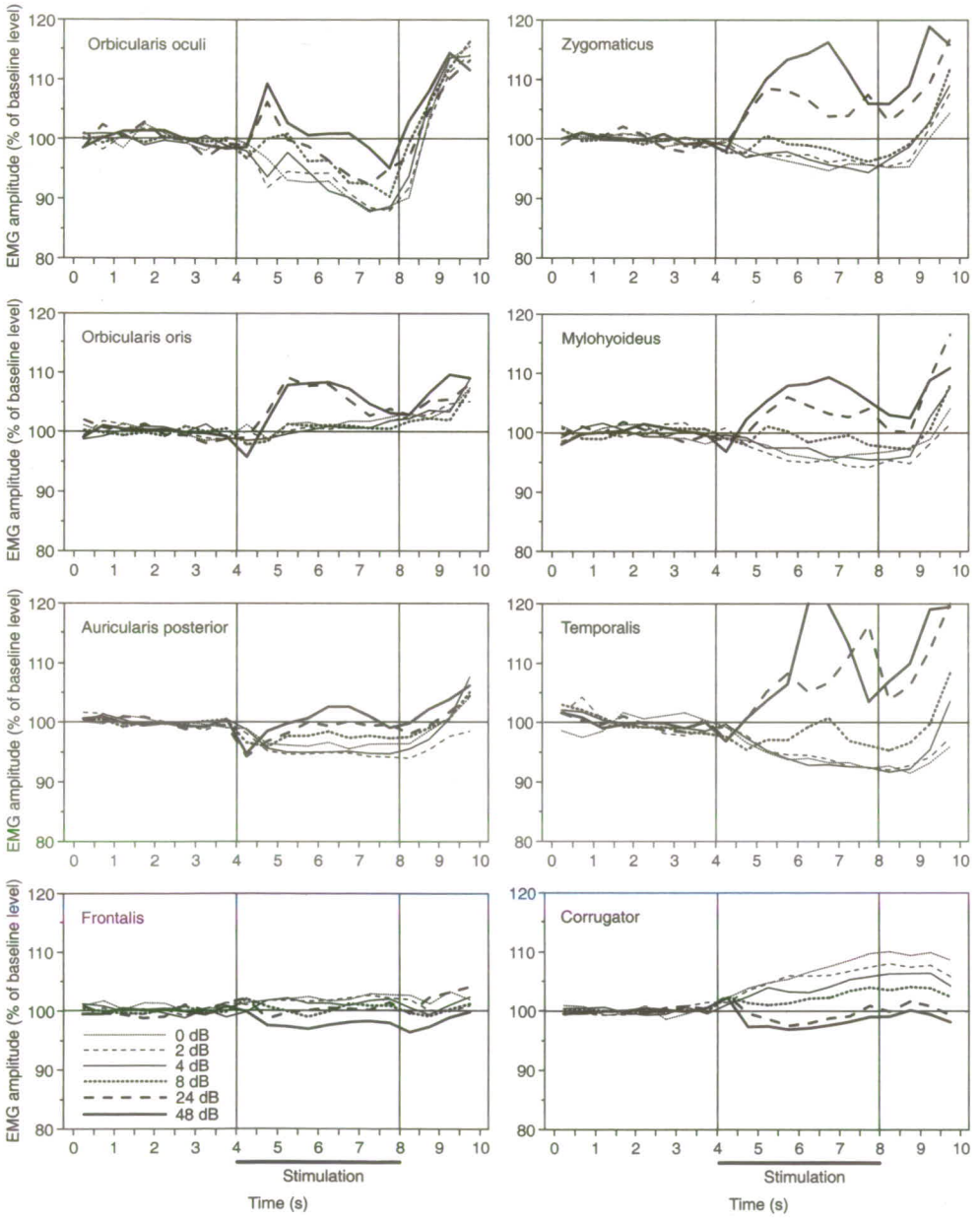

Figure 6.3. Mean EMG responses elicited by auditory stimuli of varying intensity.

Thus, only orbicularis oculi displayed an overall inhibition of EMG activity. In the other three muscles, occurence of EMG inhibition depended on stimulus intensity. Figure 6.3 shows that whereas EMG activity in temporalis, zygomaticus, and mylohyoideus was inhibited at the four lowest stimulus intensities, it was facilitated at the two highest intensities. Facilitation at the highest intensities together with inhibition at the lowest intensities nullified the overall effect of auditory stimulation on the EMG activity level. In fact, in these muscles, a clear dissociation existed between the EMG amplitude at the two highest and the four lowest intensities. Therefore, the overall effect of auditory stimulation on EMG amplitude was tested separately (two-tailed) for the two loudest and the four weakest stimuli. For the four weakest stimuli, an overall inhibition of EMG activity was found for temporalis, $F(1,23) = 24.46$, $p < .001$, zygomaticus, $F(1,23) = 17.82$, $p < .001$, and mylohyoideus, $F(1,23) = 18.22$, $p < .001$. The two loudest stimuli caused an overall facilitation of EMG in zygomaticus, $F(1,23) = 10.56$, $p < .01$, and mylohyoideus, $F(1,23) = 5.89$, $p < .05$.

EMG activity of frontalis and corrugator was expected to be facilitated during stimulus presentation. However, the overall EMG amplitude of frontalis during the last 3 s of stimulus presentation did not significantly differ from baseline level. Nevertheless, we found a negative linear relationship between EMG amplitude and stimulus intensity, $F(1,23) = 4.51$, $p < .05$. Overall EMG amplitude of corrugator was significantly larger than baseline, $F(1,23) = 10.31$, $p < .01$, and decreased linearly with stimulus intensity, $F(1,23) = 38.17$, $p < .001$.

For orbicularis oris and auricularis posterior, no specific expectations were formulated about the direction of EMG responses during stimulus presentation. For orbicularis oris, we found an overall facilitatory effect on EMG activity during the last 3 s of stimulation, $F(1,23) = 7.93$, $p < .01$. In accordance with the results of the other muscles in the lower part of the face, EMG amplitude was lower at the four weakest than at the two highest stimulus intensities. The two loudest stimuli caused EMG activity to be significantly elevated above baseline level, $F(1,23) = 10.44$, $p < .01$, whereas EMG at the four weakest stimuli did not significantly deviate from baseline. We did not find a significant linear relationship with stimulus intensity. For auricularis posterior, we observed the same pattern of results as for the majority of pericranial muscles. Overall mean EMG amplitude during the last 3 s of the stimulus was inhibited, $F(1,23) = 10.11$, $p < .01$, and increased curvilinearly with stimulus intensity, linear $F(1,23) = 5.37$, $p < .05$, quadratic $F(1,23) = 8.34$, $p < .01$.

In summary, EMG activity was inhibited in lower facial muscles (with exception of orbicularis oris), masticatory muscles, and auricularis posterior when weak auditory stimuli were presented. In addition, inhibition became stronger when stimulus intensity approached the auditory threshold. In upper facial muscles (frontalis and corrugator), EMG activity reversed from inhibition to facilitation when stimulus intensity was gradually diminished to threshold level.

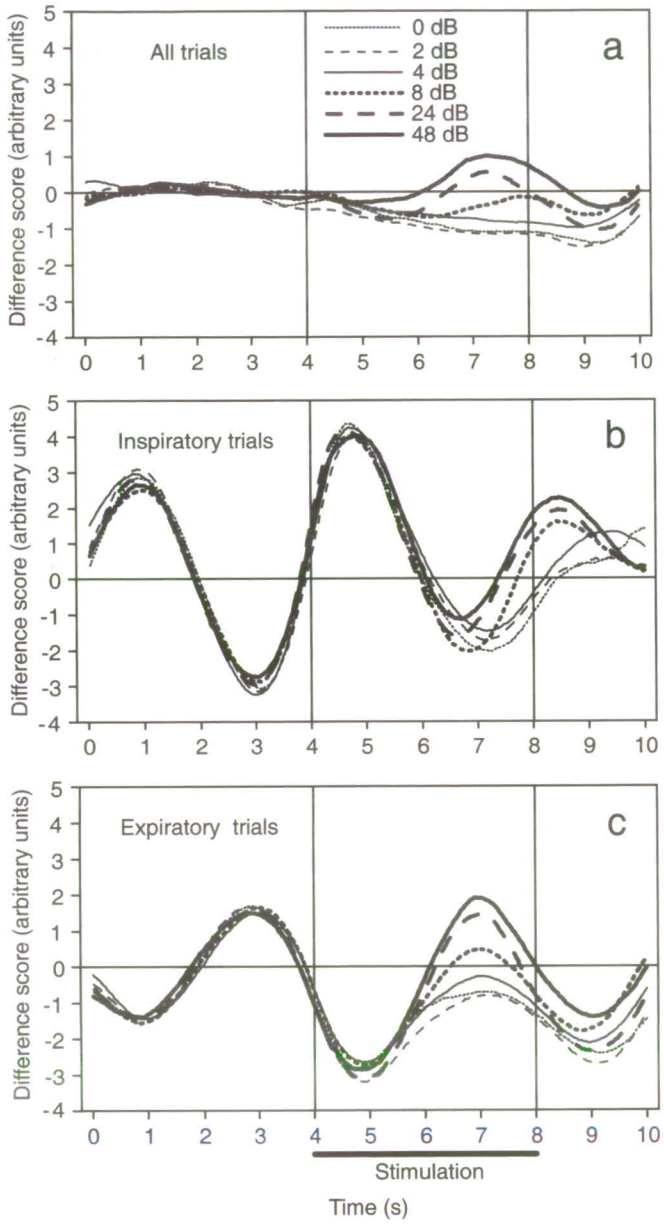

Figure 6.4. (a) Mean respiratory responses elicited by auditory stimuli of varying intensity. Upward deflections indicate inspiration. (b) and (c) Mean respiratory responses for stimuli presented during inspiration and expiration phase, respectively.

Stimulus detection in relation to EMG baseline level

According to our hypothesis, inhibition of EMG activity of lower facial and masticatory muscles increases auditory sensitivity. It might therefore be expected that a relatively high absolute level of EMG activity just before stimulus onset would increase auditory

threshold whereas a relatively low EMG level would increase the probability of detecting a faint auditory stimulus. To test this hypothesis, mean prestimulus baseline EMG activity levels during trials with undetected stimuli in the three weakest stimulus conditions (0, 2, and 4 dB(A) SL above threshold) were compared with baseline EMG levels during trials with detected stimuli. In the four muscles for which EMG inhibition during stimulus presentation was a priori expected, mean baseline EMG activity appeared to be higher when stimuli were not detected than when they were detected, that is, in temporalis, $F(1,23) = 6.17, p < .01$, orbicularis oculi, $F(1,23) = 7.18, p < .01$, zygomaticus, $F(1,23) = 5.77, p < .05$, and mylohyoideus, $F(1,23) = 6.45, p < .01$. A relationship appeared thus to exist between relatively low baseline EMG levels in these muscles and the ability to detect faint auditory stimuli. In the other muscles, such a significant relationship between baseline EMG activity and stimulus detection was not found.

Respiration

In Figure 6.4a, mean respiratory responses associated with the different auditory stimulus intensities are shown. Auditory stimulus presentation clearly modified respiratory activity. First, the effects on the amplitude of the respiratory response will be presented. Overall, peak respiratory amplitude responses were significantly smaller than zero, $F(1,23) = 7.76, p < .01$, indicating an overall expiratory response during auditory stimulation. As shown in Figure 6.4a, during stimulus presentation, there was a tendency to expiration for the weakest stimuli and inspiration for the strongest stimuli. This was confirmed by a curvilinear trend of peak respiratory amplitude across stimulus intensities (linear trend: $F(1,23) = 28.71, p < .001$, quadratic trend: $F(1,23) = 5.41, p < .05$). To get more insight into the contribution of inspiratory and expiratory trials to the effect of stimulus intensity on the respiratory response, average responses were determined for inspiratory trials and expiratory trials separately, representing on average 36% and 64% of the total number of trials, respectively. Figures 6.4b and 6.4c, respectively, show that the effect of stimulus intensity on the amplitude of respiration was relatively small during inspiratory trials whereas during expiratory trials, weaker stimuli had an incremental inhibitory effect on the next inspiration.

Next, the effect of stimulus intensity on respiratory period was investigated. The respiratory period that included stimulus onset was significantly longer than the period immediately preceding stimulus onset, $F(1,23) = 73.01, p < .001$. This prolongation effect decreased when stimuli became louder as indicated by a significant negative linear trend, $F(1,23) = 18.71, p < .001$ (Figure 6.5). This inverse linear relationship was mainly caused by a differentiation in expiration time rather than inspiration time as was revealed by a significant difference between the linear trends of inspiration and expiration time across stimulus intensity, $F(1,23) = 18.45, p < .001$. Figure 6.5 shows that expiration time linearly decreased with stimulus intensity, $F(1,23) = 17.19, p < .001$, whereas inspiration time did not significantly change with stimulus intensity.

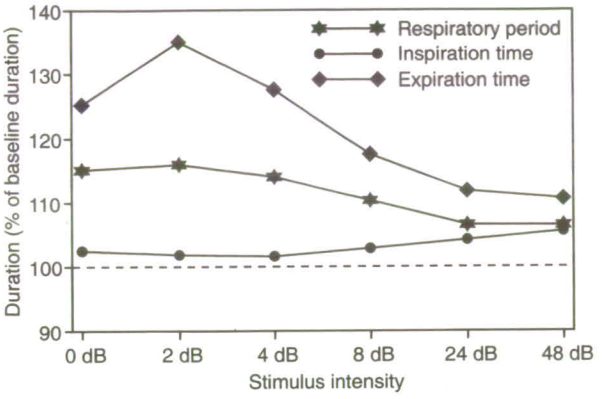

Figure 6.5. Mean respiratory period, inspiration time, and expiration time as a function of auditory stimulus intensity.

Summarizing, auditory stimuli with intensities near hearing threshold level produced a net expiratory response whereas stimuli well above threshold level produced a net inspiration. The tendency of expiration with presentation of weak stimuli was mainly caused by suppression of inspiration following stimuli presented during the inspiration phase. Auditory stimulation resulted in a prolongation of the respiratory period that could be attributed to prolongation of expiration time. This effect became weaker with stronger stimulus intensities.

Heart rate

In Figure 6.6a, heart rate changes associated with the different auditory stimulus intensities are shown. Overall, stimulus-related peak heart rate changes indicated a significant deceleration in comparison with baseline, $F(1,23) = 44.63$, $p < .001$. As shown in Figure 6.6a, there was a tendency for heart rate deceleration during the weakest stimuli and acceleration during the strongest stimuli. Peak heart rate change varied curvilinearly with stimulus intensity as revealed by significant linear, $F(1,23) = 78.89$, $p < .001$, and quadratic trends, $F(1,23) = 11.51$, $p < .05$. As shown in Figures 6.6b and 6.6c, categorizing heart rate responses into inspiratory and expiratory trials revealed a clear respiratory sinus arrhythmia during the baseline period that to some extent, persisted during the period of stimulus presentation. However, during both inspiratory and expiratory trials, the baseline pattern of respiratory sinus arrhythmia was strongly modulated by the effects of auditory stimulation, with a tendency for increasing deceleration with weaker stimulus intensity.

In conclusion, stimulus presentation elicited a tendency for heart rate deceleration during both inspiratory and expiratory trials that was inversely related to stimulus intensity.

6.3.3 Discussion

The modulation of auditory stimulus intensity elicited similar patterns of change in EMG activity of widespread pericranial muscles, respiration, and heart rate. Stimulus intensities near threshold were associated with inhibition of EMG activity of lower facial, masticatory, and auricularis posterior muscles; suppression of inspiration and slower breathing; and bradycardia; whereas stimulus intensities well above threshold resulted in raised EMG levels, increased inspiration, and heart rate acceleration. Stimulus intensities and physiological response levels were proportionally related as indicated by significant linear trends. These results support the hypothesis that the physiological responses are functional for the recognition of auditory stimuli that are difficult to detect or discriminate. In the introduction, we presented a series of empirical arguments from the literature suggesting that this functional mechanism consists of two different components: (a) lowering of internal muscular and respiratory noise, resulting in less interference with external auditory stimuli, and (b) relaxation of middle ear muscles concurrent with relaxation of pericranial muscles, resulting in lower auditory thresholds for low-frequency sounds. The EMG data from four different muscles also more directly testified to this functionality through the inverse relationship between prestimulus baseline EMG levels and the sensitivity to subsequently presented weak auditory stimuli.

EMG activity during stimulus presentation was not in all investigated muscles positively related to auditory stimulus intensity. As expected, corrugator and, to a lesser extent, frontalis EMG activity were negatively related to stimulus intensity. This relationship might be an indication of increasing effortful attention to stimuli of decreasing intensity. A positive relationship between facilitatory corrugator EMG responses and the difficulty of an auditory pitch discrimination task was earlier reported by Cohen, Davidson, Senulis, Saron, and Weisman (1992). In general, increased attention during perceptual and cognitive tasks is reflected by increased EMG activity in corrugator and frontalis (e.g., Kjellberg, Sköldström, Tesarz, & Dallner, 1994; Van Boxtel & Jessurun, 1993). The raised EMG activity in corrugator during presentation of weak stimuli was probably not intrinsically related to improved auditory sensitivity. This notion is indirectly supported by the result that prestimulus baseline EMG activity did not differ between trials with detected and undetected stimuli, unlike lower facial and masticatory muscles, for which baseline EMG activity appeared to be related to stimulus detection.

The EMG activity of orbicularis oris was not significantly inhibited during stimulus presentation and thus formed a clear exception in comparison with the other lower facial muscles. In previous studies using warned reaction time paradigms, inconsistent results were found for this muscle. During the anticipation of an auditory or visual reaction signal, Van Boxtel et al. (1996) found a significant EMG facilitation whereas Van Boxtel, Veldhuizen, & Waterink (1998) as well as Waterink (1997) consistently observed a significant inhibition throughout a series of experiments. We think that

with the current electrode placements for orbicularis oris, EMG might be picked up from different muscles showing opposite response patterns: orbicularis oris showing inhibition and mentalis showing facilitation. This hypothesis needs further investigation.

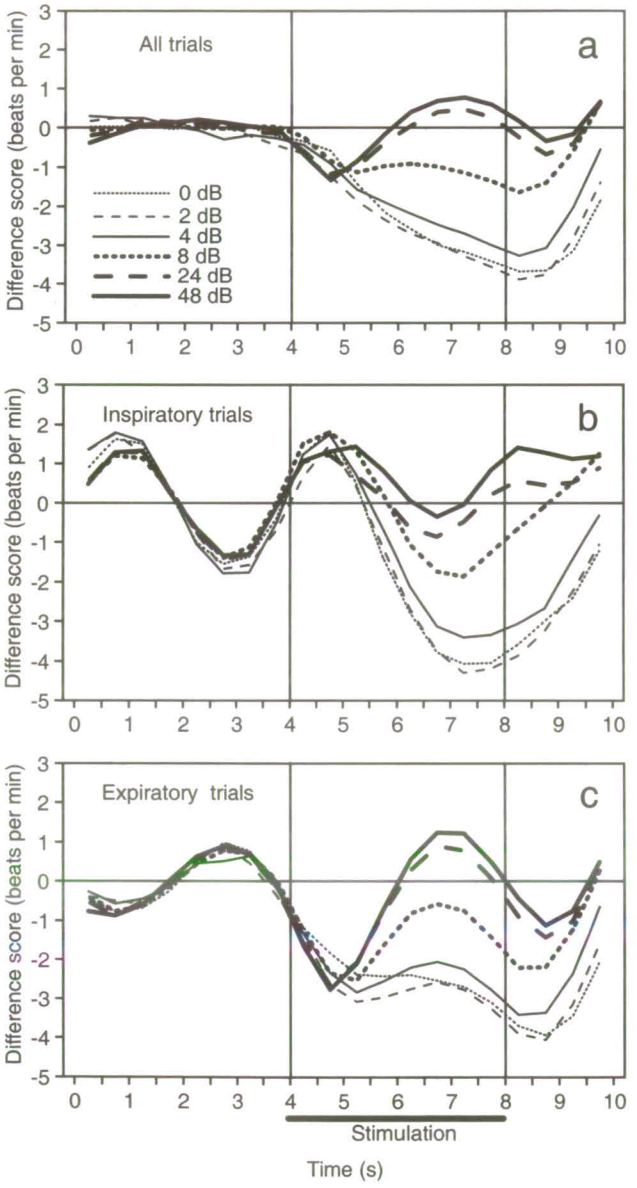

Figure 6.6. (a) Mean heart rate responses elicited by auditory stimuli of varying intensity. (b) and (c) Mean heart rate responses for stimuli presented during inspiration and expiration phase, respectively.

We have seen that the coherent pattern of pericranial EMG inhibition, suppression of inspiration, and bradycardia reversed into EMG facilitation, increased inspiration, and heart rate acceleration when stimulus intensity was clearly elevated above threshold value. There is some indication that this reversal was caused by an early recognition of the two loudest tones (24 and 48 dB(A) SL above threshold). The EMG recordings of orbicularis oculi show a clear short-latency transient response to the two loudest tones (Figure 6.3). Inspection of the mean EMG recordings with a higher temporal resolution revealed response latencies of 740 and 620 ms, respectively. Considering these relatively long latencies, it is unlikely that this response was a startle blink reflex. Earlier studies using auditory and visual discrimination tasks suggest that this EMG burst reflects a endogenous blink following stimulus recognition (Fukuda & Matsunaga, 1983; Goldstein, Walrath, Stern, & Strock, 1985). Endogenous eye blinks are suppressed when visual or auditory stimuli are anticipated to prevent interference with stimulus detection. They are postponed until stimulus processing has been completed (Goldstein et al., 1985). The latencies of the blink responses in our recordings suggest that the two loudest tones were detected in a relatively early stage of presentation. When stimuli were presented that were more difficult to discern, suppression of blinks was continued throughout stimulus presentation (Figure 6.3). In the two strongest stimulus intensity conditions, there was also a reversal of heart rate deceleration into acceleration shortly following stimulus onset (Figure 6.6a). This can be considered another sign of stimulus recognition, in conformity with results of Cohen et al. (1992), who observed that heart rate deceleration during a pitch discrimination task reversed into acceleration following detection of a change in pitch.

Many studies have shown that during warned reaction time tasks, physiological responses might not only be related to stimulus anticipation but also to preparation of motor response execution. In our experiment, preparation of response execution does not seem a relevant factor in explaining the physiological responses during auditory stimulation. First, unspeeded responses were produced as indicated by the relatively long responses latencies. Second, response execution cannot explain the observed effect of stimulus intensity on the physiological response patterns. A more likely alternative hypothesis is that the physiological responses were related to the anticipation of stimulus offset that served as an imperative response signal. This would explain why at the weakest stimulus intensities, inhibition of respiration, heart rate, and EMG activity in the majority of muscles as well as facilitation of corrugator EMG continued to progress until stimulus offset. With weak stimuli, stimulus offset was difficult to discern, leading to uncertainty about offset time. This uncertainty might be reflected in the reaction times which increased when stimuli became weaker (Figure 6.2). The prolonged physiological responses during stimulus presentation may thus not necessarily be associated with detection of the ongoing stimulus but, rather, with detection of stimulus offset. However, this explanation still allows us to interpret the physiological responses in terms of facilitation of perceptual input rather than in terms of motor

preparation because also in this view prolonged pericranial and respiratory inhibition would favor detection of stimulus offset.

To gain more direct evidence of the influence of pericranial muscle contractions on auditory sensitivity, a second experiment was conducted in which we tested whether deliberately performed pericranial muscle contractions would impair auditory sensitivity. Weak sound stimuli of different perithreshold intensities were presented while the participants performed a constant, voluntary contraction of the zygomaticus muscle assisted by visual feedback of the EMG signal. This muscle was chosen because it belonged to the muscles showing inhibition during weak auditory stimuli and because static contraction of this muscle can be sustained for a relatively long time in comparison with contraction of other muscles showing an inhibitory response in Experiment 1 (Van Boxtel, Goudswaard, Van der Molen, & Van den Bosch, 1983). Stimulus detection during zygomaticus contraction was compared with detection during two different control conditions in which contraction of corrugator or first dorsal interosseus was performed. Contraction of corrugator was used as a control condition because, on the basis of the results of Experiment 1, we did not expect that increased corrugator EMG would impair auditory sensitivity. Contraction of first dorsal interosseus, a small hand muscle, was introduced to control for negative effects on stimulus detection due to the attention demanded by the feedback-controlled regulation of zygomaticus contraction.

6.4 EXPERIMENT 2

6.4.1 Method

Participants

Eight healthy female and four male volunteers with a mean age of 22.0 years (range 19–26 years) participated in this experiment. Only persons with normal hearing and not wearing glasses were allowed to participate. None of the persons participated in Experiment 1.

EMG recording and feedback

EMG was recorded from the right zygomaticus, corrugator, and first dorsal interosseous muscles using the same methods as in Experiment 1. For recordings from the first dorsal interosseous, EMG electrodes were placed 15 mm apart on the belly of the muscle. Contraction of this muscle was standardized by squeezing the extremities of a small wooden rod that was held between thumb and index finger. Participants learned to selectively contract zygomaticus and corrugator, aided by instructions of the experimenter and observing their faces in a mirror. The maximal EMG output (EMG_{max}) of each muscle was determined by letting participants perform a maximal contraction of about 4 s. This procedure was repeated several times and the average of the maximal EMG amplitudes was taken as EMG_{max}. Visual feedback of the EMG activity of the

contracting muscle was provided by means of a display placed 2 m in front of the participant. For that purpose, the EMG signal was full-wave linearly rectified and low-pass filtered (–3 dB cut-off frequency at 1 Hz). A green light signal indicated whether the amplitude of the smoothed, rectified EMG signal was at a level between 10 and 30% of EMG_{max}. Higher and lower contraction levels were indicated by two distinct red lights that were located above and below the green light, respectively.

Experimental task and procedure

As we have explained above, negative effects of pericranial muscle contractions on auditory sensitivity may particularly be expected for low-frequency sounds (< 1000 Hz). To test this hypothesis, tones of 100 and 1500 Hz were presented through a loudspeaker placed behind the subject. Deviating from Experiment 1, headphones were not used because they appeared to amplify the acoustic noise generated by the pericranial contractions, in particular zygomaticus contraction. Auditory stimuli had a duration of 1 s and linear rise and fall times of 100 ms. As auditory threshold may be considered independent of stimulus duration when the latter is larger than 200–500 ms (Scharf & Buus, 1986), stimulus duration was not a relevant factor for detection performance.

Each participant adhered to two experimental sessions on two separate days. On one day the 100-Hz tones were presented and on the other one the 1500-Hz tones in a counterbalanced order. Stimulus onset asynchronies were equally distributed between 6 and 18 s in steps of 3 s and had a mean of 12 s. Before the start of the experiment, the individual hearing threshold was determined using a staircase procedure. Stimulus intensities relative to threshold level were –2, –1, 0, 1, 2, 3, 4, 5, 6, and 7 dB(A) SL. As in Experiment 1, participants were instructed to indicate detection of a stimulus by performing an unspeeded response, using a response button held in the left hand. A short training session followed in which participants learned to maintain the contraction level in each muscle at 20 ± 10% of EMG_{max}. Subsequently, the experimental session started. Within trial blocks of 8 min duration, four stimuli of each intensity level were presented in a random order, under the restriction that two consecutive stimuli were of different intensities. During a trial block, a contraction was performed of either the zygomaticus, corrugator, or first dorsal interosseous muscle at the target EMG level. For each contraction condition, two trial blocks were presented resulting in eight stimuli per intensity level per muscle. The order of the six trial blocks was systematically varied across participants, under the condition that different muscles had to be contracted during two successive blocks. Before the first trial block and following the last one, there was a resting period of 6 min in which baseline EMG activity was recorded from the three muscles. Participants were instructed to relax and keep their eyes closed.

EMG signals of the three muscles were continuously recorded during the three contraction conditions and the baseline periods. The signals were used to check off-line

whether the participants correctly performed the contraction tasks and if EMG levels during contraction substantially surpassed those of baseline.

Data analysis

The number of detected stimuli was counted for each muscle contraction condition. Two difference contrast scores were calculated: the number of stimuli detected during zygomaticus contraction minus that detected during contraction of corrugator or first dorsal interosseus. Both contrast variables were subjected to a MANOVA for repeated measures, with pitch (100 Hz vs. 1500 Hz) and stimulus intensity (varying from –2 to 7 dB) as within-subject variables. A 5% significance level was adopted in all tests. One-tailed tests were applied to evaluate whether the difference contrast scores significantly deviated from zero because the direction of the differences was predicted a priori. Two-tailed tests were applied for the effects of pitch and stimulus intensity as well as their interactions.

6.4.2 Results and discussion

Figure 6.7a shows the percentage of detected 100-Hz and 1500-Hz tones per stimulus intensity level. The number of detected stimuli did not significantly differ between experimental and control conditions, neither between zygomaticus and corrugator nor between zygomaticus and first dorsal interosseous. However, the difference between zygomaticus and first dorsal interosseous was significantly influenced by pitch, $F(1,11) = 5.98$, $p < .05$. Simple effect tests showed that 100-Hz tones were detected significantly less during contraction of zygomaticus than during contraction of first dorsal interosseous, $F(1,11) = 4.09$, $p < .05$, but that 1500-Hz tones were detected equally frequent in both conditions.

Summarizing, contraction of zygomaticus at 20% of EMG_{max} had no significant influence on the detection of 1500-Hz tones but significantly less 100-Hz tones were detected in comparison with contraction of first dorsal interosseous. Although such a significant effect was expected, particularly for low-frequency tones, the effect size was small. In addition, the expected difference in stimulus detections between zygomaticus and corrugator contraction conditions was not confirmed. These results thus do not unambiguously confirm our hypotheses. We should reckon with the possibility that the expected direct and indirect negative effects of zygomaticus contraction on auditory sensitivity are only revealed at higher contraction levels. Therefore, an additional experiment was carried out in which contraction levels of zygomaticus and corrugator were increased to 50% of EMG_{max}. As facial muscles are generally very resistant to fatigue, such relatively strong contractions can be sustained for longer periods without problems. Median endurance times obtained for contractions at 50% of EMG_{max} were 10.5 min for zygomaticus and 26.3 min for corrugator (Van Boxtel et al., 1983).

The contraction level of the first dorsal interosseus muscle was maintained at 20% of EMG_{max} given the relatively fast fatigability of this muscle in comparison with facial

muscles and the much greater difficulty of attaining the stronger force level. It was found that a constant, isometric contraction of this muscle at 50% of maximum force could, on the average, be sustained not longer than 88 s (Zijdewind, Kernell, & Kukulka, 1995) whereas an endurance time of 534 s was obtained for a contraction at 20% of maximum force (Fuglevand, Zackowski, Huey, & Enoka, 1993). In the current study, contraction of the first dorsal interosseus was primarily introduced as a control for negative effects of the contraction regulation task on stimulus detection. Given this purpose, contraction at the 20% level seemed more adequate than a physically exhausting contraction at the 50% level so we decided to maintain the contraction level at 20% of EMG_{max} in Experiment 3.

6.5 EXPERIMENT 3

6.5.1 Method

Nine healthy female and three male volunteers with a mean age of 21.3 years (range 18–25 years) participated in this experiment. Only persons with normal hearing and not wearing glasses were allowed to participate. None of the persons participated in Experiment 1 or 2.

Physiological recordings, experimental task, procedure, and data analysis were identical to those in Experiment 2 with a few differences. In the current experiment, the contraction level for zygomaticus and corrugator was increased to 50% of EMG_{max}. The duration of each trial block was reduced to 4 min to prevent strong fatigue. To obtain a sufficient number of trials per stimulus intensity level within such a short period, the two highest stimulus intensities were left out which resulted in eight different intensity levels (–2, –1, 0, 1, 2, 3, 4 and 5 dB(A) SL), each presented six times within each of the three contraction conditions.

6.5.2 Results and discussion

Figure 6.7b shows the percentage of detected 100-Hz and 1500-Hz tones per stimulus intensity level. Overall, the number of stimuli detected during contraction of zygomaticus was smaller than during contraction of corrugator, $F(1,11) = 4.74, p < .05$, and also smaller than during contraction of first dorsal interosseus, $F(1,11) = 14.93, p < .01$. However, both the former, $F(1,11) = 7.13, p < .05$, and the latter difference, $F(1,11) = 9.09, p < .05$, were significantly dependent on pitch. As is suggested by visual inspection of Figure 6.7b, simple effect tests showed that the significant differences were confined to the 100-Hz tones. These tones were significantly less frequently detected during contraction of zygomaticus than during contraction of corrugator, $F(1,11) = 18.96, p < .001$, or first dorsal interosseus, $F(1,11) = 7.35, p < .01$. For 1500-Hz tones, significant differences between zygomaticus contraction and the two control conditions were not found.

Summarizing, contraction of zygomaticus at 50% of EMG_{max}, in comparison with

contraction of corrugator or first dorsal interosseus, had a negative effect on the auditory threshold for 100-Hz tones but did not negatively affect the threshold for 1500-Hz tones. The observed difference with the two control conditions supports the conclusion that the effect is specifically connected to certain pericranial muscles and that, at least, it cannot be completely explained by attentional resources demanded by the contraction regulation task.

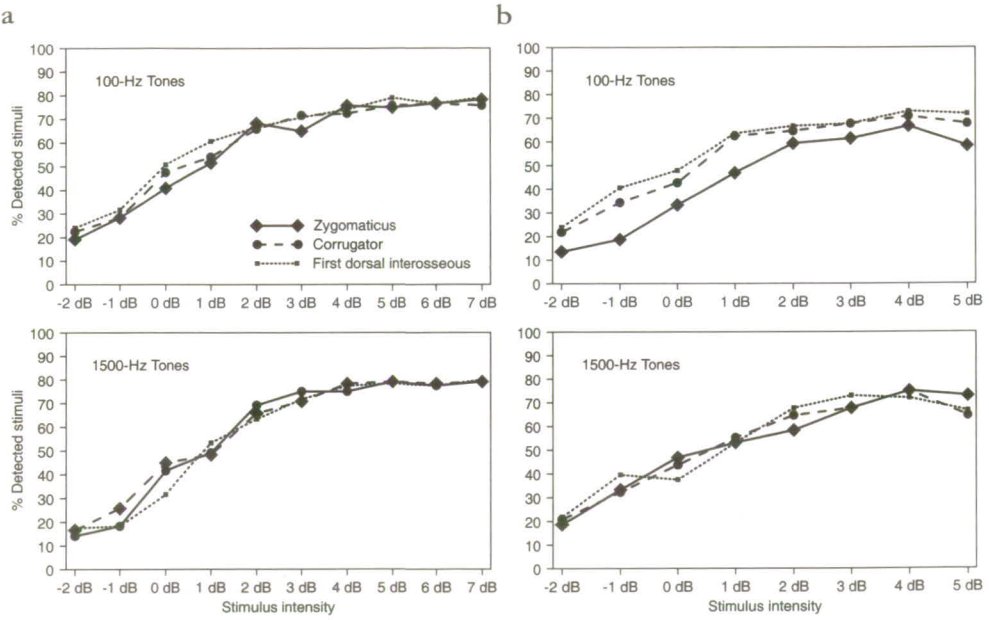

Figure 6.7. (a) Mean percentage of detected 100-Hz and 1500-Hz tones as a function of auditory stimulus intensity during steady, voluntary contractions of zygomaticus, corrugator, and first dorsal interosseus at a level of 20 ± 10% of EMG_{max}. (b) The same during contractions of zygomaticus and corrugator at a level of 50 ± 10% of EMG_{max}, and first dorsal interosseus at a level of 20 ± 10% of EMG_{max}.

6.5.3 General discussion

The functionality of inhibitory pericranial muscle responses

The results of Experiment 3 are consistent with those of Experiment 1. The opposite approaches of both experiments provide converging evidence for our hypothesis that muscular inhibition during weak auditory stimulation facilitates recognition of low-frequency sounds and, on the other hand, that contraction of pericranial muscles negatively affects the perceptual sensitivity for such sounds. Critically considering the evidence for the latter conclusion, however, we may doubt the ecological validity of the voluntary zygomaticus contraction because sustained contractions of this muscle at 50% of EMG_{max} cannot be expected to be a frequent event during daily life. However, the re-

sults imply that impairment of auditory sensitivity may also be expected during dynamic contractions exceeding the 50% level. Such contractions frequently occur during natural movements such as swallowing, chewing, yawning, sucking, licking, and emotional expressions. This deduction is supported by the negative effect of increased prestimulation EMG activity on auditory sensitivity as observed in Experiment 1.

Our results are consistent with earlier studies demonstrating that sensitivity for low-frequency tones can be trained. Subjects could learn to lower the threshold for 100-Hz tones by 16 dB by being absolutely still, avoiding even slight head motion or breathing (Loeb & Dickson, 1961; Zwislocki, 1958). We have argued in the introduction that avoiding such activities also reduces synkinetic activities of middle ear muscles. Simmons (1964) hypothesized that a major function of such synkinetic responses in man and animal might be reducing the sensation of air- and bone-conducted low-frequency noise produced by the organism itself and thus preventing this noise from masking external sounds of higher frequencies. He presents the example of a grazing deer whose internal noise level from both chewing and head motion is attenuated so that it remains sensitive to the higher pitched sounds signifying the approach of a predator. Inhibition of middle ear and pericranial muscle activity, together with inhibition of heart rate and respiration, might be a functional response pattern during voluntary or involuntary attention to external stimuli. These responses might be intrinsic components of the generalized orienting response. Sokolov (1963) considers the enhancement of the sensitivity of sensory modalities as the primary function of the generalized orienting response, including that of the peripheral receptors. He refers to work by Maruseva and Chistovich demonstrating that during the occurrence of somatomotor responses indicating an orienting response, the threshold for auditory stimuli was lowered by 10–12 dB (p. 13).

Interrelationships between pericranial, respiratory, and cardiac inhibitory responses

Experiment 1 showed clear interrelationships between EMG, respiratory, and cardiac responses as a function of auditory stimulus intensity. Decreasing stimulus intensity produced larger EMG inhibition (in masticatory and lower facial muscles), EMG facilitation (in upper facial muscles), respiratory inhibition, and heart rate deceleration. In this respect, a certain discrepancy should be noted with the earlier study by Van Boxtel et al. (1996) of stimulus anticipation processes. In this study, it was also found that larger heart rate deceleration was related to larger EMG inhibition in the majority of investigated muscles but, on the contrary, they found that EMG facilitation in upper facial muscles became smaller when heart rate deceleration increased. An important methodological difference with the current study, however, is that they reported interrelationships between physiological responses across trial blocks associated with variations in stimulus and response modality (visual vs. auditory stimuli, hand vs. foot responses) whereas the current study addressed interrelations within trial blocks associated with variations in stimulus intensity. Stimulus and response modality may

have been confounding variables, hampering a direct comparison of physiological interrelationships between both studies.

Although the current study focuses on the functionality of pericranial EMG responses during voluntary attention or involuntary orienting to external stimuli, these responses seem to be closely connected with respiratory and heart rate responses. When discussing the mechanism underlying this integrated response pattern, several issues seem important. First, the question arises whether the different physiological responses are determined by a single control mechanism or whether they are controlled by separate mechanisms that are only loosely coupled. Related to this issue, it should be discussed whether interrelationships between different response systems can be explained by causal, peripheral feedback loops or by a common dependency on a central control mechanism. Second, assuming that physiological response systems play a functional role in sensory sensitivity, the question is whether in this respect somatomotor, respiratory, and cardiac response systems are equally relevant or whether a certain response system is of primary importance, the other ones being of secondary importance or irrelevant. These issues have been discussed repeatedly in the psychophysiological literature, in particular the interrelationship between somatomotor and cardiac responses during sensory intake processes. We will only reiterate here the most relevant points for the current study.

Based on their observation that heart rate decelerates in conjunction with somatomotor inhibition in periocular and perioral regions during the anticipation of an aversive stimulus or a reaction signal, Obrist and his colleagues formulated their influential *cardiac-somatic coupling* hypothesis (for an overview see Obrist, 1976, 1981; Obrist, Webb, Sutterer, & Howard, 1970a). This hypothesis implies that during passive expectancy situations, task-irrelevant motor activities are inhibited in order to prevent competition with forthcoming task-relevant sensory or motor activities. In such situations, heart rate seems to be almost exclusively under vagal control and is rapidly adjusted to potential changes in the metabolic demands of the motor system. Motor inhibition and heart rate deceleration are directly interrelated due to an integrated feedforward control at the level of the central nervous system. If motor inhibition is of brief duration, the real metabolic changes will be trivial so that afferent metabolic feedback signals from the muscles will not play a significant role in the heart rate deceleration.

The cardiac-somatic coupling hypothesis presumed that inhibition of irrelevant activities is generalized to the entire skeletomotor system. Later studies of other investigators, however, could not confirm this hypothesis for muscles in leg, arm, shoulder, neck, and forehead regions and found that its validity was limited to eye movements and activities of masticatory and lower facial muscles (Brunia & Vingerhoets, 1980; Haagh & Brunia, 1984, 1985; Van Boxtel et al., 1996). The results of the current study agree with such a regional constriction of the cardiac-somatic coupling hypothesis and suggest that the hypothesis is not only valid for voluntary attention to imminent stimuli but also for involuntary orienting to an actual stimulus. In the opinion of

Obrist and his colleagues, the functionality of cardiac-somatic inhibition with regard to sensory intake would primarily depend on motoric inhibition with heart rate deceleration being a secondary response. Heart rate deceleration during a warned auditory reaction time task could be prevented by means of vagal blockade but significant effects on reaction time and somatomotor inhibition were not found (Obrist, Webb, Sutterer, & Howard, 1970b). The authors concluded that heart rate deceleration was not causally involved in the facilitation of behavioral performance. It may also be concluded that heart rate changes were not responsible for motoric inhibition but that both responses could be considered independent peripheral effects controlled by a central mechanism. Results obtained within a different behavioral context also suggest that parallel changes in pericranial muscle activity and heart rate were not causally related through peripheral feedback loops (Kettunen, Ravaja, Näätänan, & Keltikangas-Järvinen, 2000). Cross-correlations between phasic changes in heart rate and EMG activity in frontalis, corrugator, and zygomaticus during the administration of a Rorschach test showed that EMG responses preceded heart rate responses with an approximate time lag of 2 s, which is too short for cardiac control by metabolic feedback signals from the contracting muscles.

We may next consider to what extent the control of somatomotor inhibition and bradycardia within the context of sensory intake situations is integrated with the control of respiratory inhibition. As shown in Figures 6.6b and 6.6c, weak auditory stimuli presented during either inspiration or expiration induced a bradycardia that was superimposed on the steady-state respiratory sinus arrhythmia. A similar effect was earlier found by Turpin and Sartory (1980). The question is to what extent the stimulus intensity dependent heart rate decelerations were determined by changes in the respiratory pattern. The respiratory response patterns depicted in Figures 6.4b and 6.4c show a good correspondence with the heart rate responses, in particular during the expiratory trials (constituting 64% of the total number of trials). Bradycardia and suppression of inspiration showed parallel increases with decreasing stimulus intensity. Bradycardia during active or passive orienting to auditory stimuli is majorly caused by an increase in vagal cardiac activation (e.g., Obrist et al., 1970b; Quigley & Berntson, 1990; Saiers, Richardson, & Campbell, 1989). In a broad overview of respiratory mechanisms affecting central vagal cardiac control, Berntson, Cacioppo, and Quigley (1993) showed that vagal control is strongly influenced by central respiratory generators and afferent impulses from pulmonary stretch receptors. Central and peripheral respiratory determinants of heart rate are closely entrained and may not be readily dissociated in intact, waking subjects. Changes in heart rate due to changes in respiratory period and volume (e.g., Grossman, Karemaker, & Wieling, 1991; Grossman & Kollai, 1993) may thus be based on both central and peripheral mechanisms. Even in the absence of notable respiratory movements, cardiac vagal control may be modulated by intrinsic central respiratory rhythms (Berntson et al., 1993). Central respiratory generators could be involved in the heart rate deceleration persisting during

stimulus anticipation when breathing was voluntarily controlled or suspended (Iacono & Lykken, 1978; Obrist et al., 1969). The tight central integration of respiratory and vagal cardiac control mechanisms annihilate at this moment a discussion of to what extent the observed respiratory and cardiac inhibition were causally related through peripheral feedback loops or could be considered parallel effects of an integrated central control mechanism.

As far as we know, there is also not much insight into the mechanisms underlying the coordination of the observed respiratory and pericranial inhibitory responses. Porges (1995) hypothesizes a coordination between pericranial muscular responses and cardiac and respiratory control at the level of brain stem cranial nerve nuclei. He discusses evolutionary and embryological arguments for a functional integration between the activity of the vagal motor nuclei and those of the trigeminal, facial, glossopharyngeal, and accessory cranial nerves, resulting in a coordination of breathing and heart rate with ingestive behaviors, vocalization, and facial expression. This system might be responsible for the respiratory rhythms that have been observed in intracellular recordings from motoneurons in the facial nucleus (Huangfu, Koshiya, & Guyenet, 1993) and in EMG activity of oropharyngeal and tongue muscles (e.g., Sauerland, Orr, & Hairston, 1981; Sauerland, Sauerland, Orr, & Hairston, 1981). Although solid empirical evidence is lacking, we hypothesize that, given the multiplicity of functions of cranial motor systems, cardiorespiratory and pericranial muscular control systems are only loosely coupled. As a supporting result, Obrist et al., (1969) found that voluntary control or suspension of breathing during stimulus anticipation did not prevent inhibition of periocular and perioral motor activity, nor did it prevent heart rate deceleration.

The functionality of respiratory inhibition during active or passive orienting to auditory stimuli remains uncertain. However, the increasing respiratory inhibition in proportion with decreasing stimulus intensity supports Darwin's hypothesis (1872) that it serves to suppress internal noise to facilitate auditory perception.

Chapter 7

Pericranial muscular, respiratory, and heart rate components of the orienting response*

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7.1 Abstract

We have earlier found that voluntary attention to weak auditory stimuli induces inhibition of respiration, heart rate, and electromyographic (EMG) activity of masticatory and lower facial muscles and that these responses lower the auditory threshold for low-frequency sounds. In the current study, we examined whether this inhibitory response pattern also occurs during involuntary orienting to novel, nonsignal sounds. Environmental sounds of low intensity were presented unexpectedly during the performance of a reading task. Orienting responses (ORs) were elicited as indicated by heart rate deceleration and skin conductance responses. Inhibitory respiratory and pericranial EMG responses appeared to be intrinsic components of the OR. Together with the autonomic responses, they habituated when a nonsignal auditory stimulus was repeatedly presented. Our results also suggest that eye and pinna movements occurred toward the sound source. The results of the current study are consistent with the hypothesis of Sokolov (1963) that the primary function of the OR is enhancement of sensory sensitivity.

7.2 Introduction

The orienting response was probably first mentioned by Pavlov (1927) under the term *investigatory reflex* or "what-is-it? reflex." It was defined as an immediate response in man and animals to the slightest change in the world around them, evoking an orientation of the appropriate receptor organ allowing full investigation of the agent bringing about the change. Sokolov (1963, 1969) elaborated this definition in his conception of the generalized orienting response as a complex of automatic, preattentive changes in brain activity and peripheral reflex responses to unexpected, novel changes in the environment. The orienting response would be directed to a nonselective enhancement of the sensitivity of sensory modalities, including that of the peripheral receptors, resulting in facilitation of the uptake, transmission, and analysis of environmental information. With regard to the peripheral reflex responses, Sokolov made a distinction between direct effects on the receptor and indirect effects in the form of (1) "tuning of the receptor" by eye, pinna, and head movements, (2) inhibition of gross bodily movements and respiration, and (3) autonomic changes (for example vascular and electrodermal responses). Besides the generalized orienting response to a nonsignal stimulus, Sokolov proposed the existence of a so-called local orienting response during active attention to a signal stimulus, implying the limitation of sensory benefits to the sensory modality of the signal. Sokolov's thesis regarding the sensory function of the orienting response was not parallelled by convincing empirical evidence. In Soviet studies, only some fragmentary evidence was presented of decreased sensory thresholds during the occurrence of an orienting response (Sokolov, 1963; Voronin, Leontiev, Luria, Sokolov, & Vinogradova, 1965).

Also in the Western literature, the asserted sensory function of the orienting response has not much been clarified (cf. Graham, 1997; Spinks & Siddle, 1983). The

large majority of studies concerned the effects of physical parameters of brief, simple sensory stimuli on physiological responses, in particular heart rate, electrodermal responses, and brain potentials. A few studies have investigated overt behavioral responses that might subserve stimulus detection and processing. Such behavioral responses can be classified into two categories: (1) stopping of ongoing activity, probably with the purpose of preventing irrelevant activities competing with sensory activities, and (2) directing the sense organs toward the source of stimulation through eye, pinna, or head movements. In animals, such initial responses to novel stimuli can be found in different species, for example in cat (Sanford, Ball, Morrison, Ross, & Mann, 1992; Sanford, Morrison, Ball, Ross, & Mann, 1993), rat (Evans & Hammond, 1983; Nivison, Ursin, & Gjestland, 1984; Saiers, Richardson, & Campbell, 1990; Walasek, Węsierska, & Zieliński, 1994; Zieliński, 1966), birds (Gabrielsen, Blix, & Ursin, 1985), and mole (Aitkin, Horseman, & Bush, 1982). In human newborns, various behaviors were observed on presentation of novel stimuli, such as reduced activity, suppression of sucking, widening of the eyes, visual fixation, and head turning toward the stimulus (Graham, Anthony, & Zeigler, 1983). Eye movements toward visual stimuli were also found in children (Mackworth & Otto, 1970) and adults (Verbaten, Woestenburg, & Sjouw, 1979). Graham (1984, 1992) proposed a distinction between (1) the transient-detecting response, consisting of short-latency, brief responses to transient onset aspects of low-intensity stimuli, and (2) the orienting response, consisting of longer-latency, sustained responses to steady-state aspects of such stimuli. The slowly-habituating transient detecting response, permitting rapid detection of a stimulus and its location, includes receptor-directing movements such as saccadic eye movements and head turns and is associated with brief slowing of heart rate. The rapidly-habituating orienting response, directed to identification or discrimination of the stimulus, is associated with a general reduction in motor activity and sustained slowing of heart rate.

The current study was undertaken to examine whether novel, unexpected stimuli elicit physiological and behavioral changes which might be related to the hypothesized sensory function of the orienting response. We focused on two physiological response systems that have received little or no attention in the study of the orienting response so far: respiration and activity of pericranial muscles innervated by the trigeminal and facial nerves. In several older publications, it was asserted that during orienting to a sudden auditory stimulus there is a partial or complete inhibition of breathing, reducing disturbing respiratory sounds (Gratiolet, 1865; Darwin, 1872; Woodworth, 1938). Later studies indeed demonstrated instantaneous slowing of breathing to nonsignal auditory stimuli of low or moderate intensity (Barry, 1977; Graham et al., 1983; Poole, Goetzinger, & Rousey, 1966; Rousey & Reitz, 1967). In the last two studies, inhibition of breathing became stronger the more stimulus intensity approached the auditory threshold. Van Boxtel, Damen, and Brunia (1996) proposed a similar functional role of inhibition of pericranial muscle activity during stimulus intake. They observed inhibition of electromyographic (EMG) activity in masticatory

muscles and in muscles in the lower part of the face during the anticipation of auditory or visual reaction signals. They hypothesized direct and indirect positive influences of this relaxation on auditory sensitivity, in particular for low-frequency sounds. The direct effect would imply a suppression of the low-frequency internal sound vibrations that are generated by the asynchronous, unfused twitch contractions of the active motor units (Orizio, 1993). These sounds might be transmitted to the inner ear via bone conduction and constitute a background noise negatively affecting the auditory sensitivity to external signals. Indirectly, pericranial inhibition might be expected to be accompanied by relaxation of middle ear muscles (Djupesland, 1965; Klockhoff, 1961; Salomon & Starr, 1963), producing lower auditory thresholds, especially for low-frequency sounds (Reger, 1960; Smith, 1943). Van Boxtel et al. also found that EMG inhibition was proportionally related to inhibition of heart rate.

Stekelenburg and Van Boxtel (2001) (chapter 6 of this thesis) found evidence for a functional role of respiratory and pericranial muscular inhibition during auditory stimulus intake. In an auditory signal detection task, presentation of stimuli at the subjective detection threshold level or slightly higher levels (0–8 dB SL) elicited inhibition of respiration, heart rate, and EMG activity in lower facial muscles (orbicularis oculi and zygomaticus major), masticatory muscles (temporalis and mylohyoideus), and the auricularis posterior muscle. Inhibitory responses became stronger with weaker stimulus intensities. The authors argued that these inhibitory responses would raise the chance of stimulus detection. Respiration, heart rate, and EMG activity were facilitated when stimulus intensities were amply above threshold level (24 dB SL and 48 dB SL). EMG responses in upper facial muscles (frontalis and corrugator) showed an opposite pattern: a tendency to increasing facilitation with weaker stimulus intensities and a tendency to inhibition at the two strongest intensities (24 dB SL and 48 dB SL). This response pattern was interpreted as reflecting an increase in effortful attention when stimulus detection became more difficult. Two findings strengthened the presumed relationship between auditory sensitivity and spontaneous EMG activity in masticatory and lower facial muscles. First, stimuli of near-threshold intensities were better detected when prestimulus EMG levels in these muscles were low. Second, in a subsequent experiment, a deliberately controlled steady contraction of zygomaticus produced an increase in auditory threshold for 100-Hz tones compared with contraction of corrugator or first dorsal interosseus (a small hand muscle).

The study of Stekelenburg and Van Boxtel (2001) may provide a clue with regard to the presumed sensory function of autonomic and motor components of the orienting response. It leads to the prediction that pericranial and respiratory inhibition occurs during the presentation of a nonsignal auditory stimulus in order to quiet down somatic noise that might interfere with the detection and identification of the stimulus. Such an inhibitory response pattern may particularly be expected in case of stimulus properties facilitating the occurrence of a generalized orienting response: unexpectedness, novelty, complexity, low to moderate intensity, and a not too brief duration (Bohlin,

Graham, Silverstein, & Hackley, 1981; Graham, 1979, 1984, 1992; Sokolov, 1963; Spinks & Siddle, 1983; Turpin & Siddle, 1983; Turpin, Schaefer, & Boucsein, 1999).

In the current study, pericranial EMG activity, respiration, heart rate, and skin conductance response (SCR) were recorded during the presentation of unexpected, weak auditory stimuli with a high degree of novelty and complexity. Heart rate deceleration and SCR, both being considered as reliable indices of the orienting response (Cook & Turpin 1997; Graham, 1973, 1979; Graham & Clifton, 1966; Siddle, Stephenson, & Spinks, 1983), were recorded primarily to check whether the stimuli indeed elicited orienting responses. Two problems might emerge in demonstrating pericranial and respiratory inhibition as part of the orienting response. First, although we expected inhibitory responses to occur, these effects might be relatively small in comparison with the large spontaneous variations occurring in EMG activity and respiration. Second, inhibition could habituate quickly with repeated presentation of a certain stimulus. These two potential problems might hinder obtaining a significant response inhibition. To compensate for these difficulties, a stimulation paradigm was used in which strong, nonhabituating orienting responses may be expected. This was realized by presenting a series of different environmental sound samples resembling those used in earlier studies (e.g., Spencer, Dien, & Donchin, 1999; Yamaguchi, Tsuchiya, Yamagata, Toyoda, & Kobayashi, 2000). Complex novel stimuli may be expected to elicit a much deeper and more sustained heart rate deceleration than simple novel stimuli (Simons & Perlstein, 1997). Following the recommendations by Sokolov (1963) and Graham (1984), the stimuli were of low intensity and lasted at least several seconds to study the development of the long-latency, sustained orienting response. In addition, we used a more ecologically valid experimental setting as participants were engaged in a primary reading task and were not informed that stimuli would be presented occasionally (cf. Iacono & Lykken, 1983). Because of the uncertainty of the stimuli under these conditions and their high intrinsic salience, we expected that they were likely to trigger inhibitory pericranial and respiratory responses that would aid examining the stimulus. As this expectation was confirmed, a second experiment was carried out in which we investigated whether the inhibitory responses satisfied one of the most important criteria of the orienting response, namely rapid habituation with repeated presentation of the same stimulus (Graham 1973, 1979).

7.3 EXPERIMENT 1

7.3.1 Method

Participants

Twenty-two healthy right-handed volunteers (18 females and 4 males) with a mean age of 23.3 years (range 18–41 years) participated in this experiment. The participants received course credits or a monetary compensation. Because of the placement of

electrodes behind the ears to measure EMG activity from the auricularis posterior muscle, only participants who were not wearing glasses were invited.

Experimental task and procedure

Participants were seated in a comfortable armchair in a sound-attenuated and electrically shielded chamber and were instructed to carefully read a text with many factual details (an interview with the neurologist Oliver Sacks) for 30 min. They were told that after the experiment multiple choice questions about the text would be presented. To encourage attentive reading, every correct answer was rewarded with an extra monetary incentive or course credits. The participants were informed that they would not be able to read the entire 40 pages of text within the time limit so that they could opt for reading accurately or fast. The experimenter explained that the experiment involved the study of physiological processes during reading.

Auditory stimuli were produced by means of a 16 bits soundcard and emitted by a loudspeaker placed on the ground to the left of the participant at a distance of 1.5 m from the head. Participants were left unaware of the fact that sound stimuli were presented during the experiment. The loudspeaker was hidden from view in order to ascertain that they would not get suspicious about the true nature of the experiment. The stimuli consisted of 21 different environmental sounds (such as animal sounds, human talk, industrial sounds, digitally synthesized nonsense sounds, and environmental noises) that were either downloaded from the Internet or recorded in the laboratory environment. Stimulus duration varied between 4.2 and 9.2 s (M = 5.4 s, SD = 1.29 s). Stimulus intensity levels were matched across stimuli as well as possible. The maximum sound pressure level was measured with a Brüel and Kjær sound level meter (type 2237) at the position of the participant's head and ranged between 28 and 32 dB(A) rms (M = 29.2 dB, SD = 1.18 dB). The stimuli were edited so that their intensities had uniform rise and fall times of 100 ms. Stimulus onset intervals varied randomly between 50 and 100 s, in steps of 5 s, and had a mean length of 75 s. The order in which the stimuli were presented was randomized per participant. About 5 min after the experimenter signaled the start of the reading task, the first stimulus was presented.

Recording and scoring of physiological signals

Skin conductance was recorded using a constant voltage (0.5 V) coupler and Ag/AgCl electrodes with a contact area of 8 mm diameter placed on the thenar and hypothenar eminences of the left hand. The electrolyte medium consisted of a .05-M concentration of NaCl in Unibase. The skin conductance signal was filtered (DC to 8 Hz) and digitized (12 bits) at a rate of 1000 Hz. For each auditory stimulus, SCR amplitude was scored as the maximum increase in conductance (in μS) within a time window from 1 to 5 s after stimulus onset.

The electrocardiogram was measured with Ag/AgCl electrodes with a contact area of 15 mm diameter that were placed on the sternum and the precordial position V6.

The reference electrode was placed on the right scapula. The signal was relayed to a hardware R-wave detector (Mulder, 1988) that filtered the signal (–3 dB passband: 3.18–60 Hz), rectified it, and detected the R waves by triggering at the maximum slope of the electrocardiogram in the Q-R interval. The R-wave detector produced a 100-ms square wave at each R wave which was digitized at a rate of 1000 Hz. R-wave event series were converted to interbeat intervals. An artifact detection and correction procedure was applied according to the guidelines provided by Mulder (1992). Following the procedure of Graham (1978), corrected interbeat intervals were converted to heart rate (in beats per minute) for each 0.5-s interval during a 4-s prestimulus baseline period and an 8-s period following stimulus onset. The mean baseline value was subtracted from each data point to obtain the stimulus-related heart rate change. The peak value of this change (positive or negative) during the first 4 seconds of stimulus presentation was used as a measure of the magnitude of the heart rate response.

Respiration was measured by means of a respiration module that consisted of an elastic tube wrapped around the thorax just above the abdomen through which a 575-Hz tone was emitted by an oscillator that was attached to one end of the tube. Respiration caused variations in the length of the tube which were reflected by the phase difference of the tone between the oscillator and a sound-sensitive device connected to the other end of the tube. The phase difference was converted to a voltage that was digitized at a rate of 1000 Hz. The instantaneous effect of auditory stimuli on respiratory period and respiratory amplitude was analyzed. To quantify respiratory period, the same procedure was applied as in the study of Stekelenburg and Van Boxtel (2001). First, inspiration and expiration time of each respiratory cycle were determined. Inspiration time was defined as the interval between the start of inspiration and the moment of maximal inspiration (cf. Wientjes, 1992). Expiration time was defined as the interval between maximal inspiration and the start of the next inspiration. It was established whether stimulus onset occurred during the phase of inspiration (inspiratory trials) or expiration (expiratory trials). Respiratory period was determined separately for inspiratory and expiratory trials. For both types of trials, the respiratory cycle was considered to start with the respiratory phase during which the stimulus was presented (cf. Poole et al., 1966; Rousey & Reitz, 1967). This implied that for inspiratory trials the respiratory cycle began at the start of the inspiration immediately preceding stimulus onset and ended at the start of the next inspiration. For expiratory trials, respiratory period was measured from the moment of maximal inspiration immediately preceding stimulus onset to the moment of the next maximal inspiration. To quantify the effect of stimulus presentation on respiratory period, the duration of the respiratory cycle including stimulus presentation was expressed as a percentage of the duration of the cycle immediately preceding stimulus onset. Next, percent change was calculated. To assess to what extent changes in respiratory period were caused by changes in inspiration or expiration time, this quantification procedure was also applied for inspiration and expiration time separately.

Respiratory amplitude was determined separately for inspiratory and expiratory

trials. For inspiratory trials, the difference was taken between the respiratory signal value at the first maximal inspiration and the subsequent maximal expiration after stimulus onset. For expiratory trials, the difference was taken between the signal value at the first maximal expiration and the subsequent maximal inspiration. These amplitude scores were expressed as a percentage of the peak-trough amplitude during the respiratory cycle immediately preceding stimulus onset after which percent change was calculated.

Bipolar EMG activity was recorded bilaterally from seven different pericranial muscles (frontalis, corrugator supercilii, temporalis, orbicularis oculi, zygomaticus major, mylohyoideus, and auricularis posterior) and a neck muscle (sternocleidomastoideus; see Figure 7.1). On each muscle, two Ag/AgCl electrodes with a contact area of 2 mm and casing of 11 mm diameter were placed in a direction parallel to the muscle fibers with 15 mm distance between electrode centers. Details of electrode placements on pericranial muscles were presented by Van Boxtel et al. (1996) but for placement on auricularis posterior, see Stekelenburg and Van Boxtel (2001). The auricularis posterior muscle was included in this study because of its vestigial function analogous to pinna retraction in nonhuman species (Huber, 1931), presumed to attenuate the sensory impact of strong auditory stimuli. A common reference electrode for the pericranial EMG derivations (contact area 8 mm in diameter) was placed 4–5 cm above the nasion.

It was expected that lateral presentation of auditory stimuli would evoke head rotation toward the source of stimulation. We measured EMG activity of sternocleidomastoideus because this muscle is involved in contralateral rotation of the head (Costa, Vitti, De Oliveira Tosello, 1990; Mayoux-Benhamou, Revel, & Vallee, 1995). The upper electrode was placed 4 cm below the insertion of the muscle on the mastoid process. A separate common reference electrode for the left and right sternocleidomastoideus derivations was placed adjacent to the EMG electrodes on the right sternocleidomastoideus.

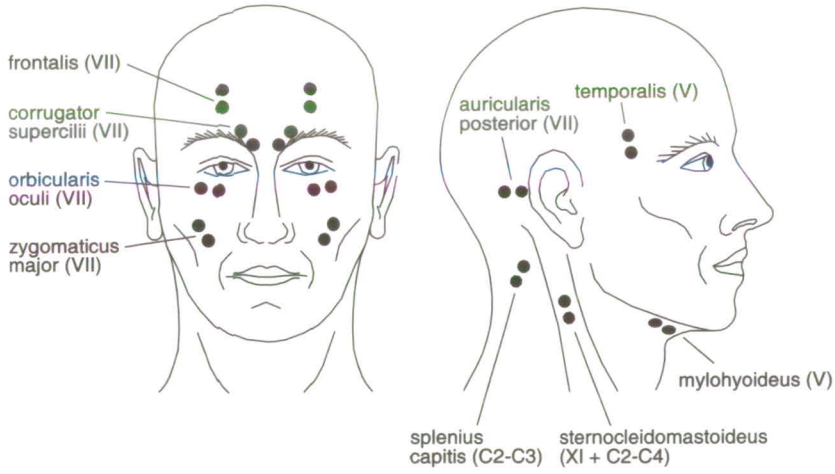

Figure 7.1. Placement of electrodes for surface EMG recordings. Roman numerals indicate muscular innervation by cranial nerves. Innervation of neck muscles by cervical spinal nerves is also indicated.

EMG signals were amplified using a low-noise medical isolation amplifier (Intronics IA296, input noise in frequency range 10–1000 Hz with 5 kΩ unbalance: 0.3 μV rms), high-pass filtered with a –3 dB cut-off frequency at 20 Hz (43 dB down/octave), low-pass filtered with a –3 dB cut-off frequency at 600 Hz (30 dB down/octave), and digitized (12 bits) at a rate of 1000 Hz. For each auditory stimulus, 12-s EMG data records were stored consisting of the 4-s prestimulus baseline period and the 8-s period following stimulus onset. EMG signals were checked off-line for gross movement artifacts associated with irrelevant activities such as yawning, stretching, coughing, and scratching. Data records were rejected when across several muscles abnormally large bursts of spontaneous EMG activity occurred that lasted at least several seconds and started within 4 s before stimulus onset. EMG signals were full-wave rectified and mean rectified EMG amplitude was calculated for 0.5-s intervals resulting in 24 data points for each stimulus presentation. Data points were expressed as a percentage of mean prestimulus baseline EMG amplitude. Finally, percent change relative to baseline was calculated. Because the shortest auditory stimulus lasted 4.2 s, the first 8 change scores after stimulus onset, corresponding to the first 4 seconds of stimulus presentation, were used as a measure of the stimulus-related EMG response (inhibition or facilitation). Before and after the reading task, EMG was recorded during a 5-min period of relaxation with eyes closed. Mean rectified EMG amplitude was calculated for both periods and averaged.

Statistical analysis

The physiological data were analyzed by means of a multivariate analysis of variance (MANOVA) for repeated measures using two slightly different designs. In the first design, with the 21 stimuli as a within-subjects variable, it was examined whether skin conductance, heart rate, and respiration showed overall inhibitory or facilitatory responses to the auditory stimuli and whether these responses habituated across the stimulus series. The physiological response scores to the 21 stimuli (i.e., SCR amplitude, peak heart rate change, percent change of respiratory period, and percent change of respiratory amplitude) were divided into seven successive blocks of three stimuli and were averaged within blocks. When a stimulation trial was rejected, the remaining response scores within a block were averaged. The block averages were entered into MANOVA. We tested whether the positive or negative response scores significantly deviated from zero. For respiratory period and respiratory amplitude, it was additionally tested whether the responses differed between inspiratory and expiratory trials. To examine habituation, we tested whether positive or negative response scores diminished across stimulation blocks. For this purpose, the block averages were transformed into linear and quadratic trend contrast scores across blocks by means of computation of orthogonal polynomials.

Similar MANOVAs were performed on the EMG responses using a somewhat more extended within-subjects design. To investigate the temporal development of inhibi-

tory or facilitatory EMG responses during stimulus presentation, time was included as a variable with eight levels, consisting of the 0.5-s averages during the first 4 seconds of stimulus presentation. The eight data points were transformed into linear and quadratic trend contrasts by means of computation of orthogonal polynomials. Another extension in comparison with the previous analysis design was that left-sided and right-sided EMG responses were tested against each other.

In all statistical analyses, a significance level of .05 was adopted. When a directional prediction could be made on the basis of theory or earlier results, one-tailed tests were applied. In all other cases, two-tailed tests were applied. Based on numerous earlier studies, it was predicted that presentation of unexpected, novel auditory stimuli of low intensity would evoke an increase in skin conductance and a deceleration of heart rate. Considering the previous results of Stekelenburg and Van Boxtel (2001), we also expected a prolongation of respiratory period, a reduction of respiratory amplitude, and an inhibition of EMG activity in the lower facial muscles (orbicularis oculi, zygomaticus), masticatory muscles (temporalis and mylohyoideus), and auricularis posterior muscle. Such a clear prediction could not be made for the upper facial muscles (frontalis and corrugator). Stekelenburg and Van Boxtel hypothesized that the facilitatory EMG responses that they found in these muscles during the presentation of barely audible sound stimuli were related to effortful attention rather than to regulation of auditory sensitivity. We could not predict whether such facilitatory responses would also occur during the present experiment in which stimulus intensities were clearly above threshold value.

A left-right difference in EMG response was only expected for the sternocleidomastoideus muscle. We expected an EMG facilitation only for the muscle on the right side due to its role in contralateral rotation of the head during stimulus presentation.

As all auditory stimuli were unique, we did not expect quick habituation of the physiological responses. Therefore, we performed two-tailed tests on the linear and quadratic trend components across stimulation blocks.

7.3.2 Results

Task performance

Multiple choice questions about the text with four response alternatives were presented. Only careful reading of the text enabled correct answering of the questions. The number of questions presented was proportional to the number of pages that were actually read. The percentage of questions that was correctly answered was on the average 77%, suggesting that the participants complied with the instructions.

Skin conductance response and heart rate

Stimulus-related SCR amplitudes were significantly larger than zero, $F(1,21) = 12.10$, $p < .01$. SCR amplitude did not significantly decrease across stimuli. Analysis of stimulus-

related peak heart rate changes indicated a significant deceleration, $F(1,21) = 76.17$, $p < .001$ (Figure 7.2). Heart rate deceleration declined linearly across stimuli, $F(1,21) = 6.90$, $p < .05$.

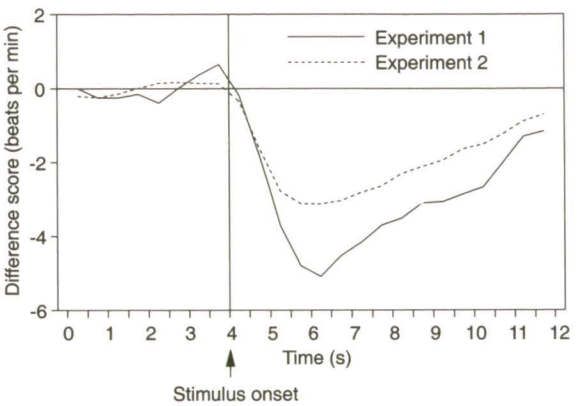

Figure 7.2. Mean heart rate responses to auditory stimuli in Experiments 1 and 2.

Respiration

Stimulus presentation induced a significant prolongation of respiratory period, $F(1,21) = 112.72$, $p < .001$ (Figure 7.3). This effect did not significantly differ between inspiratory and expiratory trials. We further examined whether a differentiation could be made between stimulus effects on inspiration and expiration time. As is illustrated in Figure 7.3, prolongation of expiration time was significantly larger than prolongation of inspiration time, $F(1,21) = 40.40$, $p < .001$. Simple effect tests revealed a significant prolongation of expiration time, $F(1,21) = 67.14$, $p < .001$, but not of inspiration time.

Respiratory amplitude was on the average not significantly affected by stimulus presentation. However, percent change of respiratory amplitude during inspiratory trials differed significantly from that during expiratory trials, $F(1,21) = 8.05$, $p < .05$. As is illustrated in Figure 7.3, stimulus presentation induced a significant reduction of respiratory amplitude during expiratory trials, $F(1,21) = 19.33$, $p < .001$, whereas for inspiratory trials there was no significant effect.

Effects of stimulus presentation on respiratory period and respiratory amplitude did not vary as a function of stimulus repetition.

EMG amplitude

Mean EMG responses to presentation of auditory stimuli are shown in Figure 7.4. First, we tested whether EMG activity during stimulus presentation deviated from baseline level. As expected, EMG activity was significantly inhibited in temporalis, $F(1,21) = 25.56$, $p < .001$, zygomaticus, $F(1,21) = 11.75$, $p < .01$, and mylohyoideus, $F(1,21) = 26.05$, $p < .001$. In addition, EMG activity of temporalis gradually declined during the

course of stimulus presentation as indicated by a significant negative linear trend over time, $F(1,21) = 11.85$, $p < .01$. Significant linear or quadratic time trends were not found for zygomaticus and mylohyoideus.

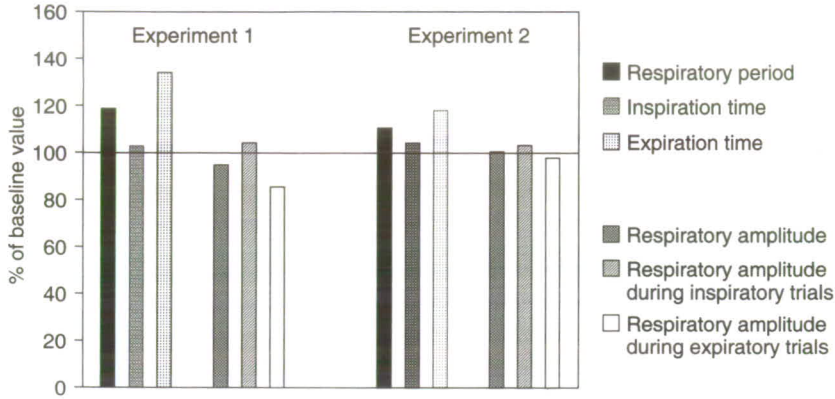

Figure 7.3. Mean responses in respiratory period and respiratory amplitude to auditory stimuli in Experiments 1 and 2.

For orbicularis oculi, the expected overall EMG inhibition during stimulus presentation was not found. Although EMG activity did not significantly differ from baseline level, it linearly increased during the course of stimulus presentation, $F(1,21) = 7.35$, $p < .05$. Neither did auricularis posterior show the expected inhibition of EMG activity. Rather, it showed a facilitation of EMG activity, $F(1,21) = 6.55$, $p < .05$ (two-tailed), which linearly declined during stimulus presentation, $F(1,21) = 5.51$, $p < .05$. Auricularis posterior was the only muscle showing a left-right difference in EMG response. EMG facilitation was larger on the left side than on the right side, $F(1,21) = 4.84$, $p < .05$. Simple effect tests showed that facilitation was significant for the left side only, $F(1,21) = 7.58$, $p < .05$. The negative linear trend during stimulus presentation was not significantly different between the two sides. Stimulus presentation failed to elicit any significant change in sternocleidomastoideus EMG.

Regarding the upper facial muscles, EMG activity of frontalis was lower than the baseline level but this difference failed to reach statistical significance. Nevertheless, EMG activity gradually declined during the course of stimulus presentation as indicated by a significant negative linear trend, $F(1,21) = 10.57$, $p < .01$. The same response pattern was found for corrugator. Also for this muscle there was an nonsignificant inhibition in EMG activity. Stimulus presentation caused a small initial facilitation of EMG activity followed by a linearly increasing inhibition, $F(1,21) = 6.47$, $p < .05$.

The second analysis concerned the habituation of EMG responses across stimulation blocks. As expected, none of the muscles showed a significant trend in EMG responses across stimuli.

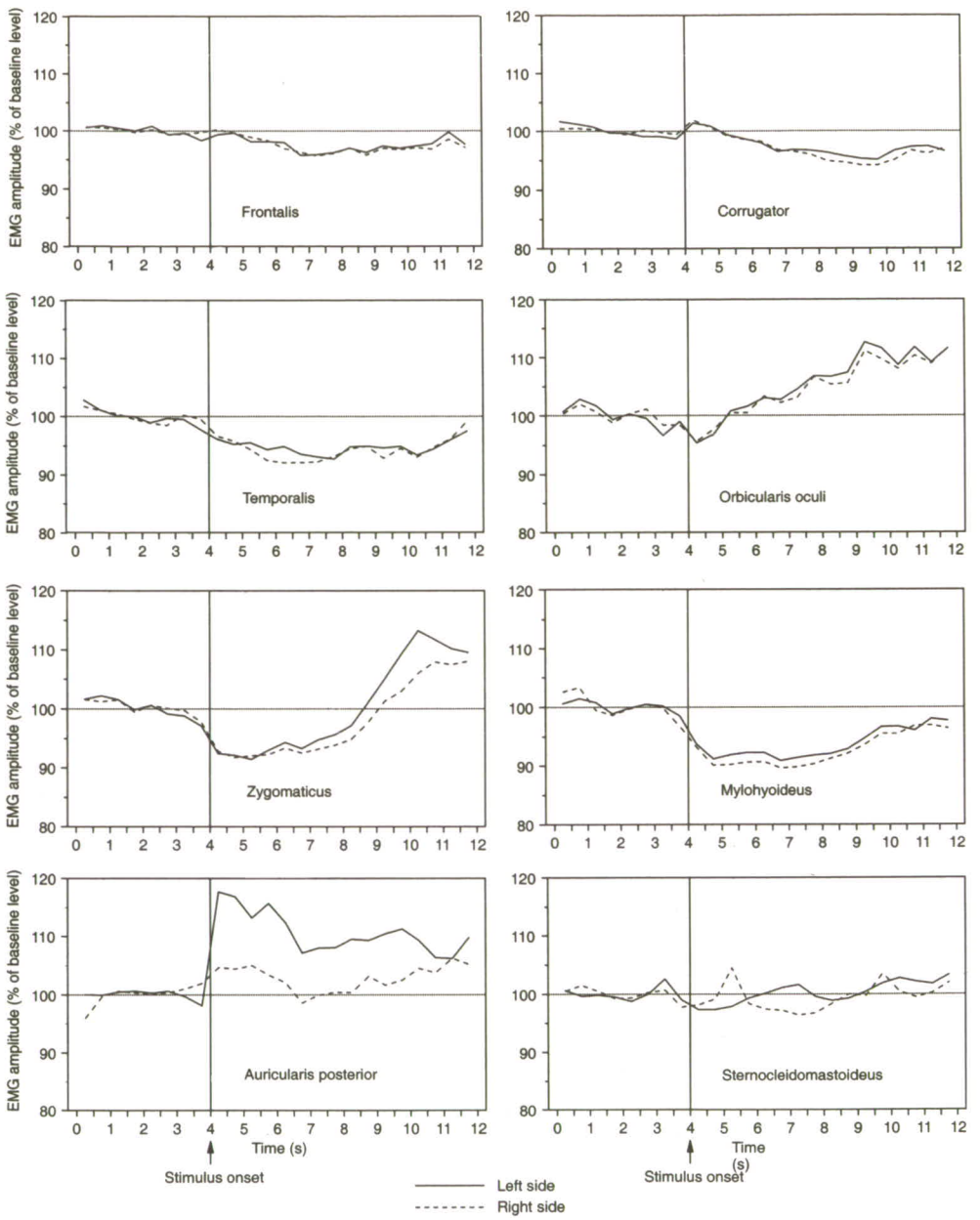

Figure 7.4. Mean EMG responses on the left and right side of the head to auditory stimuli in Experiment 1.

7.3.3 Discussion

As expected, stimulus presentations elicited orienting responses as indicated by skin conductance increase and heart rate deceleration. Orienting responses were characterized by respiratory inhibition as can be inferred from the changes in respiratory period and amplitude. The observed prolonged respiratory period indicates slowing of breathing. Respiratory amplitude during stimulus presentation was reduced when stimulus onset occurred during expiration, suggesting an inhibitory effect on the depth of the next inspiration. Suppression of breathing during unexpected, novel, weak auditory stimuli might be efficacious for the detection and discrimination of weak auditory stimuli due to a reduction of respiratory noise.

The observed pattern of EMG responses was consistent with the hypothesis that inhibition of EMG activity of masticatory and lower facial muscles during the orienting response subserves detection and identification of the auditory stimulus. EMG activity of temporalis, zygomaticus, and mylohyoideus showed a significant and sustained inhibition during stimulus presentation. It was expected that orbicularis oculi EMG would be inhibited as well, as was found in our previous study (Stekelenburg & Van Boxtel, 2001). However, this muscle only showed a transitory inhibition followed by an increasing facilitation during auditory stimulation. This unexpected finding might be explicable by taking into account the background EMG activity of this muscle during reading. To our knowledge, there are no published data about orbicularis oculi EMG during sustained reading. However, the observed suppression of endogenous eyeblinks during reading (Bentivoglio & Albanese, 1997) suggests a decrease in the excitability of orbicularis oculi motoneurons. This suppression might help to prevent interference of eyeblinks with visual input. We may expect that in conjunction with suppression of blinks, tonic EMG activity of orbicularis oculi is also inhibited. We have examined this hypothesis by comparing mean EMG activity levels during the 4-s prestimulus intervals and the two 5-min resting baseline periods. This revealed that EMG activity was significantly inhibited during the reading task, $F(1,21) = 10.20, p < .01$ (Figure 7.5), suggesting that the increasing activity of orbicularis oculi during stimulus presentation reflected a state of progressive disinhibition and a return to the resting baseline level.

EMG activity of frontalis and corrugator showed a gradual decrement during auditory stimulation. Similarly to orbicularis oculi, these responses might be related to the background activity level of these muscles during the reading task. In comparison with the resting baseline level, EMG activity was significantly enhanced during reading in both frontalis, $F(1.21) = 22.64, p < .001$, and corrugator, $F(1.21) = 17.93, p < .001$ (Figure 7.5). Enhanced tonic EMG activity in these muscles has been found earlier during tasks requiring cognitive effort (Van Boxtel & Jessurun, 1993; Waterink, 1997). The EMG responses to the auditory stimuli might thus at least partially be explained as a release of increased tonic activity associated with the cognitive task.

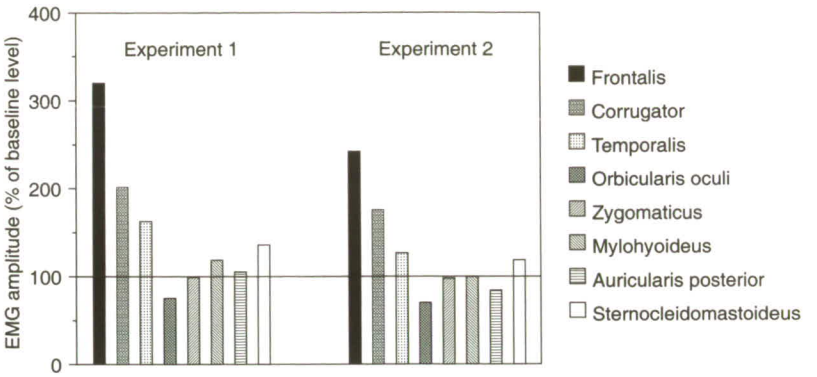

Figure 7.5. Mean EMG activity during the 4-s prestimulus intervals as a percentage of resting baseline EMG activity levels in Experiments 1 and 2.

The auricularis posterior muscle did not show the expected inhibition of EMG activity during auditory stimulation. Instead, it showed a facilitation of EMG activity on the side of stimulus presentation. This response was investigated more extensively in Experiments 3 and 4.

EMG activity of sternocleidomastoideus failed to demonstrate the expected activation contralateral to the side of stimulus presentation. An explanation might be that head rotations were absent or limited to the first few stimulus presentations. To test the latter possibility, we examined whether there was a left-right difference during the first three stimulus presentations but we did not find it. We will come back to this issue in the discussion of Experiment 3.

If the observed inhibitory responses in respiration and EMG activity were intrinsic components of the orienting response, we would expect that within individual participants the magnitude of these responses would covary with the variations in SCR and heart rate deceleration across stimulation blocks. For every participant, we therefore calculated Kendall's coefficient of concordance between the absolute changes in SCR, heart rate, respiratory period, respiratory amplitude, and EMG activity of temporalis, zygomaticus, and mylohyoideus. Fifteen participants showed a significant coefficient of concordance (for 9 participants, $p < .01$; for 6 participants, $p < .05$), 2 participants showed a tendency toward significance ($.05 < p < .10$), and 5 participants showed a nonsignificant concordance. Applying a chi-square test of combined probabilities on the participant sample (Guilford, 1965, pp. 248–250), a significant overall concordance was obtained, $\chi^2(44) = 224.37, p < .001$.

Except for heart rate deceleration, none of the physiological responses declined across the successive stimuli. Thus, we reasonably succeeded in designing a nonhabituation stimulation paradigm. Another test of the validity of the observed inhibitory muscular and respiratory responses as intrinsic components of the orienting response would be to investigate whether they habituated with repeated presentation of the same stimulus. This question was examined in the next experiment using a subset of the stimuli presented in Experiment 1.

7.4 EXPERIMENT 2

7.4.1 Method

Participants

Twenty-eight healthy right-handed volunteers (17 females and 11 males) with a mean age of 22.6 years (range 18–49 years) participated in this experiment. None of them participated in Experiment 1. The participants received course credits or a monetary compensation. Only participants who were not wearing glasses were invited.

Experimental task and procedure

Experiment 2 resembled Experiment 1 in various respects. Participants received the same instruction and performed the same task. They were again encouraged to read as much as possible of the text but now for a period of 60 min. Auditory stimuli were presented from the left side while participants were reading, the first stimulus about 5 min after the beginning of the task. A subset of seven different stimuli was taken from Experiment 1 (buzzing of a mosquito, sawing, birdsong, "wah-wah" guitar sound, pouring liquid into a vessel, stirring a cup of coffee, sounds from a typing pool). Duration of these stimuli varied between 4.3 and 5.6 s (M = 4.7 s, SD = 0.43 s). Stimulus intensities were identical to those employed in Experiment 1. Stimulus onset intervals varied randomly between 50 and 100 s, in steps of 5 s, and had a mean length of 75 s. Each stimulus was presented six times in succession, resulting in seven blocks of six identical stimuli. The order of stimulation blocks was randomized across participants. The rationale for this paradigm was that the first presentation of a certain stimulus was expected to evoke an orienting response that would habituate with repeated presentation. The orienting response was expected to recover at the first presentation of the next novel stimulus (cf. Graham, 1979).

Recording and scoring of physiological signals

Skin conductance, heart rate, respiration, and EMG activity were measured and scored in the same way as in Experiment 1. The obtained response scores were averaged across those presentations of the seven stimuli that occupied similar ordinal positions within the seven stimulation blocks. For example, the response scores following the first presentation of every stimulus were averaged. This averaging procedure was repeated for the ensuing five presentations, resulting in six ordinal averages for each physiological response measure. If stimulation trials were rejected, averaging was performed across a smaller number of stimuli belonging to a certain ordinal position.

Statistical analysis

For each physiological response measure, the six ordinal averages were entered into a MANOVA for repeated measures. As in Experiment 1, we tested whether there was an

overall inhibition or facilitation of skin conductance, heart rate, respiratory period, respiratory amplitude, and EMG amplitude during stimulus presentation, with the same directional predictions. For the EMG responses, we again tested whether they showed significant linear or quadratic trends during the course of stimulus presentation and whether there were significant left-right differences. To evaluate habituation, the six ordinal averages were transformed into orthogonal polynomial trend contrasts. Trend analyses were carried out with one-tailed tests because habituation was expected to occur for all physiological response measures.

7.4.2 Results

Task performance

The percentage of correct answers was about the same as in Experiment 1, namely 76%.

Skin conductance response and heart rate

Stimulus-related SCR amplitudes were significantly larger than zero, $F(1,27) = 18.17$, $p < .001$. SCR amplitude decreased curvilinearly as a function of repeated stimulus presentation as revealed by a significant negative linear, $F(1,27) = 11.03$, $p < .01$, and a positive quadratic trend, $F(1,27) = 5.43$, $p < .01$ (Figure 7.6).

Stimulus presentation elicited a significant heart rate deceleration, $F(1,27) = 118.81$, $p < .001$ (Figure 7.2). Heart rate deceleration diminished curvilinearly across stimulus presentations (Figure 7.6); positive linear trend $F(1,27) = 52.51$, $p < .001$; negative quadratic trend $F(1,27) = 19.38$, $p < .001$.

Respiration

Stimulus presentation evoked a significant prolongation of respiratory period, $F(1,27) = 106.04$, $p < .001$, which was independent of the respiratory phase during which the stimulus was presented (Figure 7.3). Prolongation of expiration time was significantly larger than prolongation of inspiration time, $F(1,27) = 84.91$, $p < .001$. Simple effects tests, however, showed that both inspiration time, $F(1,27) = 20.90$, $p < .001$, and expiration time, $F(1,27) = 140.89$, $p < .001$, were significantly prolonged by stimulus presentation. Prolongation of respiratory period decreased curvilinearly with stimulus repetition (Figure 7.6); negative linear trend $F(1,27) = 42.47$, $p < .001$; positive quadratic trend $F(1,27) = 7.01$, $p < .05$.

Respiratory amplitude was on the average not significantly affected by stimulus presentation nor did respiratory amplitude differ between inspiratory and expiratory trials (Figure 7.3). Presentation of a novel stimulus induced a reduction of respiratory amplitude which disappeared at subsequent presentations of the stimulus as indicated by a significant positive linear trend across stimulus presentations, $F(1,27) = 14.99$, $p < .01$ (Figure 7.6).

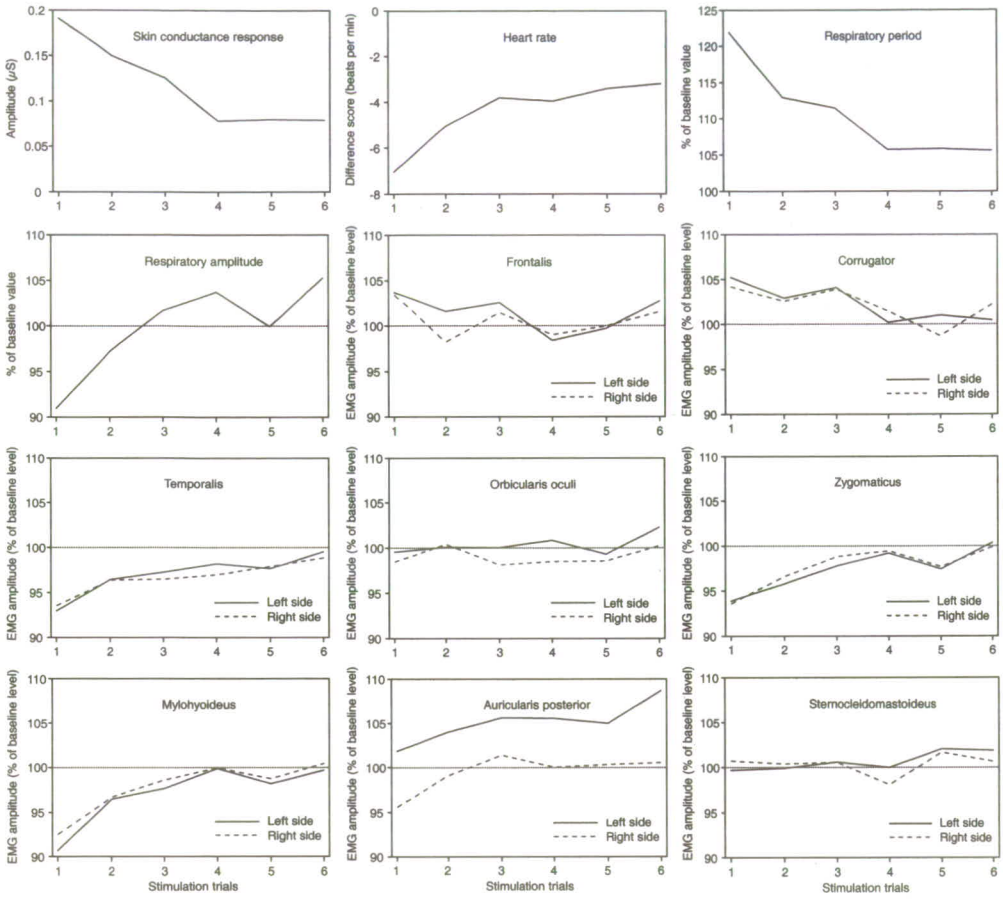

Figure 7.6. Mean responses in skin conductance, heart rate, respiratory parameters, and EMG activity to repeated presentations of auditory stimuli in Experiment 2.

EMG amplitude

The mean EMG responses to presentation of auditory stimuli are shown in Figure 7.7. Similarly to Experiment 1, we found significant inhibitory effects of stimulus presentation on EMG activity of temporalis, $F(1,27) = 14.83$, $p < .01$, zygomaticus, $F(1,27) = 13.87$, $p < .01$, and mylohyoideus, $F(1,27) = 13.89$, $p < .01$. The inhibitory response of temporalis showed a nonsignificant tendency to proceed linearly during stimulus presentation, $F(1,21) = 3.81$, $p = .06$, but systematic trends were not found for zygomaticus and mylohyoideus. Repeated presentation of the same stimulus resulted in habituation of the inhibitory responses in these three muscles as indicated by a positive linear trend for temporalis, $F(1,27) = 7.02$, $p < .05$, and zygomaticus, $F(1,27) = 8.75$, $p < .01$, and both a positive linear, $F(1,27) = 14.10$, $p < .01$, and a negative quadratic, $F(1,27) = 6.76$, $p < .05$, trend for mylohyoideus (Figure 7.6).

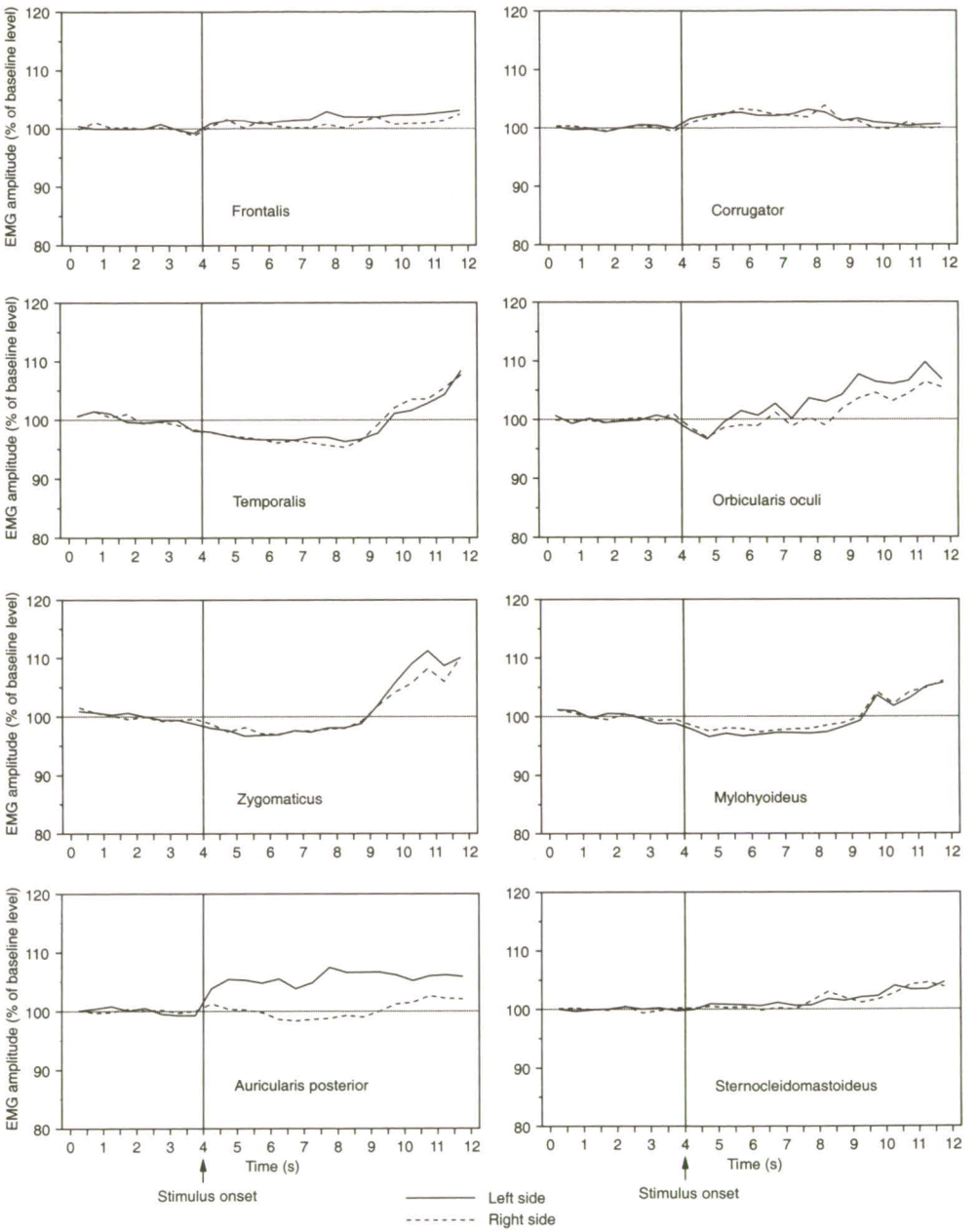

Figure 7.7. Mean EMG responses on the left and right side of the head to auditory stimuli in Experiment 2.

As in Experiment 1, EMG activity of orbicularis oculi did not significantly differ from baseline level but linearly increased during stimulus presentation, $F(1,27) = 9.16$, $p < .001$. This response pattern did not change with repeated stimulus presentation.

Rather than the expected inhibition, auricularis posterior EMG activity showed a nonsignificant tendency toward facilitation during stimulation, $F(1,27) = 3.56, p = .07$ (two-tailed). As in Experiment 1, a left-right difference in facilitatory EMG response was found, $F(1,27) = 6.04, p < .05$. When both sides were tested separately, a significant facilitation of EMG activity was found at the left side, $F(1,27) = 7.08, p < .05$, but not at the right side. Similarly to Experiment 1, the overall EMG facilitation did not habituate. Rather than a decline in EMG facilitation, auricularis posterior showed a gradual increase in facilitation with repeated presentation of the same stimuli, $F(1,27) = 5.23, p < .05$ (two-tailed), due to an increasing facilitation at the left side and a decreasing inhibition at the right side. EMG activity of sternocleidomastoideus showed a lack of response during stimulus presentation and this remained so with repeated presentation.

Of the two upper facial muscles that were examined, frontalis did not show a significant overall EMG response nor a change in response with repeated stimulus presentation. Corrugator showed a significant facilitation of EMG activity, $F(1,27) = 6.30, p < .05$, which linearly decreased with stimulus repetition, $F(1,27) = 4.38, p < .05$ (Figure 7.6).

7.4.3 Discussion

The elicitation of an increase in skin conductance and a deceleration in heart rate by a novel stimulus, and the ensuing habituation with stimulus repetition, support our conclusion following Experiment 1 that the stimuli elicited orienting responses. Again we found inhibition of respiration and EMG activity in temporalis, zygomaticus, and mylohyoideus during stimulus presentation. Also these measures showed habituation. For each participant, we calculated Kendall's coefficient of concordance between SCR, heart rate deceleration, and inhibitory respiratory and EMG responses across the six stimulus repetitions. Seventeen participants showed a significant coefficient of concordance (for 11 participants, $p < .01$; for 6 participants, $p < .05$), 2 participants showed a tendency toward significance ($.05 < p < .10$), and 9 participants showed a nonsignificant concordance. A chi-square test of combined probabilities on the participant sample revealed a significant overall concordance, $\chi^2(56) = 223.45, p < .001$. The congruency at the individual level between habituation of respiratory, EMG, and autonomic responses supports our earlier conclusion that the respiratory and EMG responses constitute intrinsic components of the orienting response. Summarizing, in both experiments the orienting response included skin conductance, heart rate, respiratory, and EMG components. Response magnitudes of these components were on the average smaller in Experiment 2 than in Experiment 1 due to habituation, as is illustrated in Figures 7.2, 7.3, 7.4, and 7.7.

As in Experiment 1, orbicularis oculi showed a short-lasting inhibition of EMG activity followed by a gradual increase in activity during auditory stimulation. This response did not habituate, supporting our earlier hypothesis that it can be considered as a release from ongoing EMG inhibition associated with reading rather than as an orienting response. As illustrated in Figure 7.5, prestimulus EMG activity in orbicu-

laris oculi during reading was also in this experiment significantly smaller than resting baseline activity, $F(1,27) = 27.27, p < .001$.

Contrary to Experiment 1, frontalis and corrugator EMG did not show a tendency to inhibition during stimulation. Rather, corrugator EMG was facilitated, a response that was also observed by Stekelenburg and Van Boxtel (2001) during the presentation of weak auditory stimuli and that was considered as an expression of voluntary attention elicited by the stimulus. The results of both experiments confirm our hypothesis that these two muscles are not involved in the orienting response and do not play a functional role in the regulation of auditory sensitivity.

As in Experiment 1, auricularis posterior showed an EMG facilitation on the side of stimulus presentation that did not habituate. It was also replicated that sternocleidomastoideus did not show the expected activation contralateral to the side of stimulus presentation. Despite the latter result, we suspected that the unexplained ipsilateral facilitation in auricularis posterior did not originate from this muscle itself but might be an artifact related to rotation of the head toward the side of stimulation. The auricularis posterior muscle is closely located to the insertions of sternocleidomastoideus and the underlying splenius capitis muscle on the mastoid process and occipital bone. Sternocleidomastoideus is involved in contralateral rotation of the head and splenius capitis in ipsilateral rotation (Costa et al., 1990; Mayoux-Benhamou et al., 1995). Theoretically, electrodes on auricularis posterior might pick up EMG activity from these two neck muscles. Although we found that sternocleidomastoideus contralateral to the left-sided stimulation was not activated, the possibility should be left open that participants performed head movements toward the stimulation side contracting the left splenius capitis only (cf. Tournay & Paillard, 1952). The increased EMG activity in the left auricularis posterior muscle may have been caused by crosstalk from the left splenius capitis. An additional experiment was conducted to disentangle the effects of stimulation side and head rotation on the EMG response of auricularis posterior. Participants deliberately performed ipsilateral or contralateral rotation of the head relative to the side of EMG recording during ipsilateral or contralateral stimulus presentation. It was examined whether the unilateral facilitation of auricularis posterior EMG could be replicated and whether ipsilateral stimulus presentation or ipsilateral head rotation were crucial for bringing about this EMG response.

7.5 EXPERIMENT 3

7.5.1 Method

Participants

Eight healthy right-handed volunteers (7 females and 1 male) with a mean age of 22.8 years (range 18–34 years) participated in this experiment. The experiment was performed under the same conditions as Experiments 1 and 2.

Experimental task and procedure

The same 21 environmental sounds as used in Experiment 1, with the same intensity, served as stimuli. Stimulus onset intervals ranged from 12 to 22 s with a mean interval of 17 s. Stimuli were presented by a loudspeaker located either to the left or to the right side of the participant. Both speakers were placed on the ground at 1.5 m distance from the head. Three marks were attached to the wall opposite to the participant which were horizontally aligned at the level of the participant's eyes. The series of 21 sounds was presented during three different behavioral conditions. Awaiting the first stimulus, the participants fixated their eyes on the middle mark. At stimulus onset, they had to change the horizontal direction of their gaze exclusively by means of head rotation. In the first condition, participants rotated their head with moderate speed to the left so that the direction of their gaze shifted from the middle mark toward the left one. They kept their head in that position until stimulus offset after which they returned to the starting position. In the second condition, the head was rotated toward the right mark. In both conditions, the angle of head rotation was 38°. In the third condition, participants fixated their eyes on the middle mark avoiding head rotation during stimulus presentation. The three conditions were combined with left-sided and right-sided stimulus presentations amounting to six different stimulation blocks, each containing the 21 sounds. The order of presentation of stimulation blocks was systematically varied between participants.

Recording and scoring of physiological signals

EMG activity was bilaterally recorded from auricularis posterior, sternocleidomastoideus, and splenius capitis muscles (Figure 7.1). Splenius capitis was located following a procedure used by Keshner, Campbell, Katz, and Peterson (1989). The upper electrode was placed 5 cm below the inferior nuchal line and the lower electrode at a distance of 15 mm in parallel with the direction of the muscle fibers. EMG activity was measured and scored in the same way as in Experiment 1. EMG was recorded from 1 s prior to stimulus onset to 5 s after stimulus onset. EMG signals were full-wave rectified and mean rectified EMG amplitude was calculated for 0.5-s intervals, resulting in 12 data points per stimulus presentation. Data points were expressed as a percentage of mean prestimulus baseline EMG amplitude. Subsequently, percentage values were averaged across stimulus presentations and percent change relative to baseline was calculated. Change scores of the left and right recording sides were averaged. The first 8 change scores after stimulus onset, corresponding to the first 4 seconds of stimulus presentation, were used as a measure of the stimulus-related EMG response.

Statistical analysis

To determine whether the augmented EMG activity in the left auricularis posterior muscle in Experiments 1 and 2 could be considered as the result of ipsilateral head rotation or ipsilateral auditory stimulation, two different analyses were carried out on

the EMG responses of the three muscles. The first analysis was performed on the data of the four stimulation blocks involving head rotation. EMG responses were analyzed by means of a MANOVA for repeated measures with two within-subjects variables: direction of head rotation (ipsilateral or contralateral relative to EMG recording side) and stimulation side (ipsilateral or contralateral relative to EMG recording side).

The second analysis was performed on the two stimulation blocks avoiding head rotation. The effect of ipsilateral versus contralateral stimulation on EMG responses was analyzed using a MANOVA for repeated measures. To investigate the temporal development of inhibitory or facilitatory EMG responses during stimulus presentation, we tested whether linear or quadratic trends were present in the eight EMG change scores. All tests were performed two-tailed.

7.5.3 Results and discussion

Figure 7.8a shows the mean EMG responses for the two head rotation and the two stimulation side conditions. Ipsilateral head rotation induced a significantly stronger EMG facilitation than contralateral rotation in both auricularis posterior, $F(1,7) = 9.15$, $p < .01$, and splenius capitis, $F(1,7) = 9.50$, $p < .01$. For sternocleidomastoideus, a significant difference in the opposite direction was found, $F(1,7) = 12.36$, $p < .01$. No significant effect of stimulation side was obtained for any of these three muscles, nor were there significant interactions between direction of head rotation and stimulation side. The relatively small but unexpected EMG activity of splenius capitis during contralateral rotation and the activity of sternocleidomastoideus during ipsilateral rotation can be explained by crosstalk of EMG potentials among these two muscles (Mayoux-Benhamou et al., 1995). Figure 7.8a shows a strong similarity in magnitude and time course between EMG responses of auricularis posterior and splenius capitis whereas auricularis posterior and sternocleidomastoideus showed divergent response patterns. These results suggest that the unilateral facilitation of auricularis posterior EMG in Experiments 1 and 2 was not a primary effect of ipsilateral stimulus presentation but was caused by crosstalk of splenius capitis EMG activity associated with ipsilateral head rotation.

In the behavioral condition in which participants did not perform head rotation during stimulus presentation, significant differences between ipsilateral and contralateral stimulus presentation were not found for any muscle (Figure 7.8b). As expected, splenius capitis and sternocleidomastoideus did not show significant EMG responses in the absence of rotational movements. Stimulation side effects in auricularis posterior were thus not found in the absence of splenius capitis activity. Based on the converging evidence from the head rotation and head fixation conditions, we provisionally conclude that the unilateral facilitation of auricularis posterior EMG in Experiments 1 and 2 was due to contamination by head movements. Under conditions of fixation of eye and head positions in frontal direction, auditory stimuli elicited a significant inhibition of auricularis posterior EMG activity, $F(1,7) = 6.30$, $p < .05$ (Figure 7.8b), which did not significantly differ between the left and right side. In

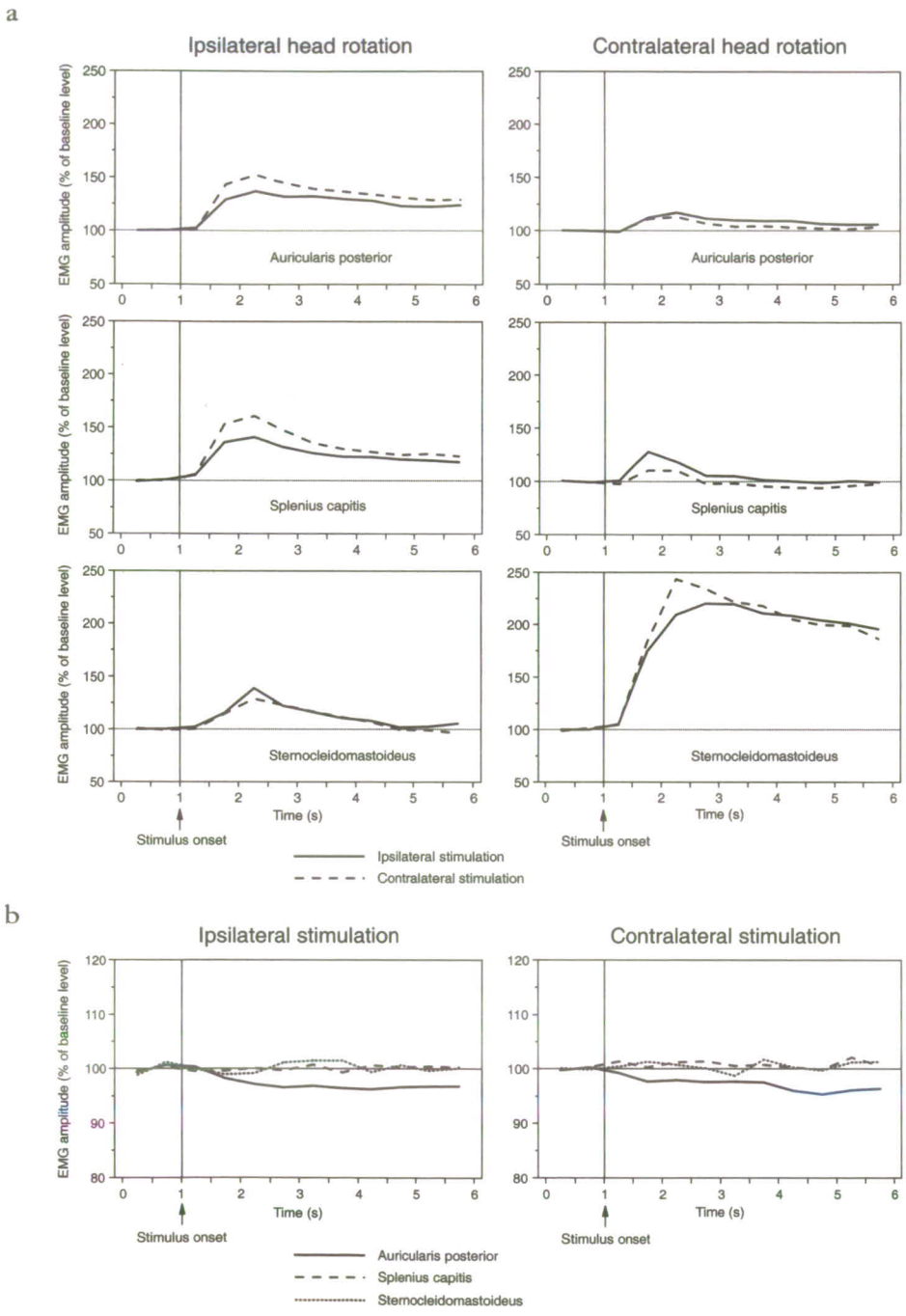

Figure 7.8. (a) Mean EMG responses to auditory stimuli presented ipsilaterally or contralaterally relative to the EMG recording side combined with ipsilateral or contralateral rotation of the head. (b) The same during absence of head rotation.

addition, the inhibition gradually increased during stimulus presentation as indicated by a significant negative linear trend, $F(1,7) = 12.89, p < .01$.

Although the clear activation of sternocleidomastoideus during contralateral rotation was in accordance with our expectation, it remains to be explained why in Experiments 1 and 2 no significant activation was found in the right sternocleidomastoideus muscle during the presumed rotational movements toward the left-sided stimulation source. In these experiments, EMG activity in this muscle might have been too small to reach the detection threshold of surface electrodes. Some support for this reasoning comes from Tournay and Paillard (1952) who observed that EMG activity of sternocleidomastoideus during free, unresisted head rotation was much smaller than that of splenius capitis. Nevertheless, an alternative explanation incorporating the absence of sternocleidomastoideus activity in these experiments should be considered. Participants could have reflexively turned their eyes toward the source of stimulation without performing head rotation. Such lateral eye movements might induce coactivation of external ear muscles, the so-called oculo-auricular phenomenon.[1] Bilateral coactivation has been demonstrated in the transversus auriculae muscle (a small intrinsic ear muscle at the dorsal surface of the pinna) synchronous with lateral gaze deviations (Schmidt & Thoden, 1978; Urban, Marczynski, & Hopf, 1993). Patuzzi and O'Beirne (1999) recorded EMG activity with one electrode on the auricularis posterior and the other on the dorsal surface of the pinna. They observed EMG facilitation during lateral rotation of the eyes toward the side of EMG recording. Unfortunately, they did not investigate whether facilitation also occurred on the contralateral side.

We conducted a second control experiment to examine whether unilateral activation of auricularis posterior, such as observed in Experiments 1 and 2, can be induced by conjugate lateral eye movements toward a laterally located source of auditory stimulation.

7.6 EXPERIMENT 4

7.6.1 Method

Participants

Twelve healthy right-handed volunteers (9 females and 3 males) with a mean age of 24.0 years (range 18–53 years) participated in this experiment.

Procedure and data analysis

Stimulus presentation, experimental procedure, recording and scoring of EMG signals, and statistical analysis were identical to those in the two head rotation conditions of Experiment 3. The only difference with Experiment 3 was the instruction. In Experi-

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[1] We wish to thank Steven A. Hackley for his useful suggestion that lateral changes in gaze direction might induce external ear muscle activity.

ment 4, participants were instructed to make horizontal eye rotations toward the same fixation points as in Experiment 3 (angle of rotation 38°) while fixating their head in frontal direction.

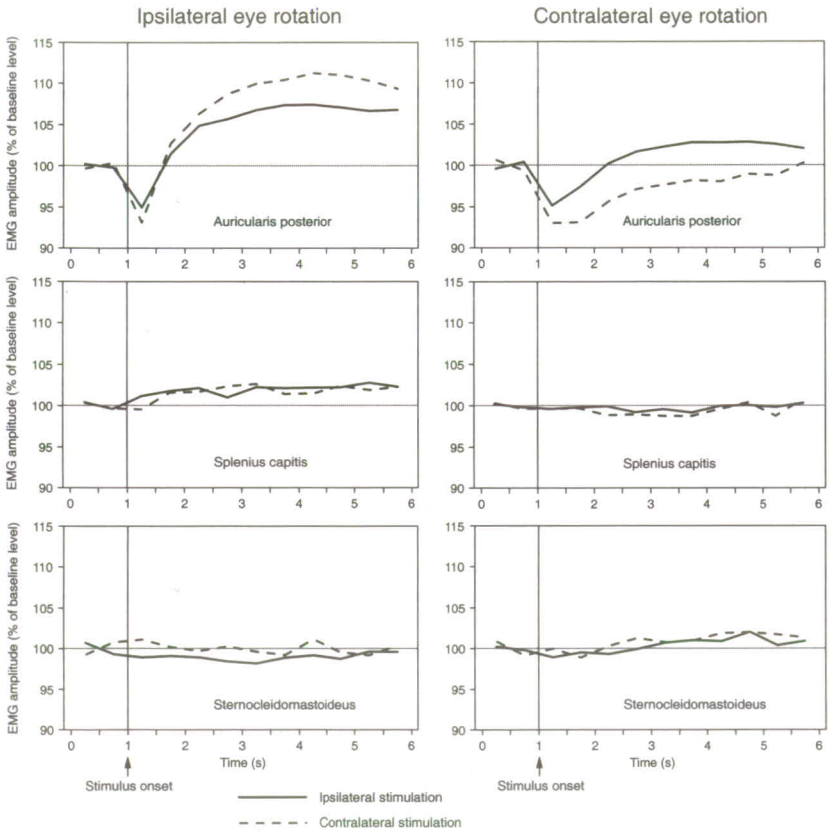

Figure 7.9. Mean EMG responses to auditory stimuli presented ipsilaterally or contralaterally relative to the EMG recording side combined with ipsilateral or contralateral rotation of the eyes.

7.6.4 Results and discussion

Figure 7.9 shows the EMG responses for both lateral eye rotation conditions. Ipsilateral eye rotation induced a significantly stronger EMG facilitation in auricularis posterior, $F(1,11) = 18.10$, $p < .01$, than contralateral rotation. During ipsilateral rotation, EMG activity was significantly elevated above the prestimulus baseline level, $F(1,11) = 8.12$, $p < .05$, whereas during contralateral rotation, EMG activity did not significantly deviate from baseline level. In both conditions, the EMG responses were preceded by a transitory inhibition of EMG activity as we have earlier observed in this muscle when

presenting weak but clearly audible stimuli (Stekelenburg & Van Boxtel, 2001) and for which we do not have an explanation.

EMG activity of splenius capitis was slightly, but significantly, larger during ipsilateral eye rotation than during contralateral rotation, $F(1,11) = 18.29$, $p < .01$. Only during ipsilateral rotation, EMG activity was significantly elevated above baseline level, $F(1,11) = 12.26$, $p < .01$. This response pattern suggests that the participants slightly rotated their head in the same direction as they rotated their eyes. However, it seems unlikely that this increase in splenius capitis EMG activity was responsible for the increase in auricularis posterior activity because the latter was several times larger than the first.

EMG activity of sternocleidomastoideus did not significantly change during eye rotation. As in Experiment 3, no significant effect of stimulation side was obtained for any of the three muscles, nor were there significant interactions between direction of head rotation and stimulation side.

The results of Experiments 3 and 4 suggest that rotational eye or head movements produce ipsilateral facilitation of auricularis posterior EMG activity. We believe that the oculo-auricular phenomenon is the best candidate to account for the ipsilateral facilitation that was found in Experiments 1 and 2. First, in Experiment 4, lateral eye rotation induced an ipsilateral facilitation of auricularis posterior EMG without synchronous facilitation of contralateral sternocleidomastoideus EMG, resembling the results of Experiments 1 and 2. Second, the ipsilateral facilitation of auricularis posterior EMG in Experiments 1 and 2 was comparable in magnitude to the facilitatory effect of eye rotation in Experiment 4 whereas it was much smaller than the effect of head rotation in Experiment 3. Altogether, our results suggest that the response of auricularis posterior during lateral presentation of weak auditory stimuli consists of two components, resembling Graham's (1984, 1992) transient-detecting and orienting responses. As demonstrated in the last condition of Experiment 3, an inhibitory orienting response can be observed in isolation under the condition that lateral eye or head movements are avoided. We have earlier observed such a sustained inhibition during binaural stimulus presentation, avoiding lateral directing movements (Stekelenburg & Van Boxtel, 2001). During lateral stimulus presentation, a transient-detecting rotational eye movement will produce an ipsilateral facilitatory EMG response in auricularis posterior that is superimposed on the inhibitory component. A differentiation between these two response components can be observed in the habituation paradigm of Experiment 2 (Figure 7.6). The left-sided stimulus elicited an inhibition in the right auricularis posterior muscle that habituated with stimulus repetition. In the left auricularis posterior, a non-habituating facilitation was superimposed on this inhibition, producing an increasing net facilitation.

From an evolutionary point of view, both response components might be functional for the detection and identification of weak auditory stimuli. The function of the inhibition can be explained by considering the auricularis posterior muscle as a vestige

derived from a postauricular muscle complex involved in pinna retraction in nonhuman species and thus actively involved in attenuating the sensory impact of strong auditory stimuli. Consistent with this idea is the occurrence in humans of short-latency reflex responses in this muscle following the presentation of strong auditory stimuli (Bochenek & Bochenek, 1976; Hackley, Woldorff, & Hillyard, 1987; Patuzzi & O'Beirne, 1999; Yoshie & Okudaira, 1969). As described by Huber (1931), humans have in common with the great anthropoid apes, such as chimpanzee and gorilla, that the external ear musculature shows a structural and functional deterioration in comparison with lower primates. Ear movements in gorilla and chimpanzee have been noted to be almost as rare as in humans. In chimpanzee and humans, the auricularis posterior muscle has been reduced to a few short muscle slips that are isolated from the strongly reduced and even vestigial occipitalis muscle. In lower primates, such as the macaques, the auricularis posterior muscle is part of a postauriculo-occipital muscle complex that produces pulling backward of the scalp and a simultaneous retraction of both ears. There is an antagonism between this muscle group and a fronto-auricular muscle complex consisting of the frontalis, auricularis anterior and superior, and orbito-auricular muscles. The orbito-auricular muscle connects the lateral part of the frontalis with auricularis anterior and superior muscles. This primitive fronto-auricular complex covers the anterior part of the cranium and one of its actions consists of erection and protraction of the pinna. In the anthropoid apes, it has divided into separate frontalis and auricularis anterior/superior muscles with strong regression of the intermediate orbito-auricular muscle. In macaques, Seiler (1973) has observed synergistic EMG activity in the muscles of the fronto-auricular complex concurrent with inactivity in the muscles of the postauriculo-occipital muscle group during attention to the environment. Huber's anatomical arguments for synergistic relationships in macaques between frontalis and auricularis anterior/superior on the one side and between occipitalis and auricularis posterior on the other hand are supported by neurophysiological studies showing that the muscles belonging to each group are innervated by motoneurons whose cell bodies are located in corresponding parts of the facial nucleus and whose axons pass through corresponding branches of the facial nerve (Jenny & Saper, 1987; Satoda et al., 1987). The antagonism between the anterior and posterior groups is also encountered in humans when during the detection of very weak auditory stimuli an inhibition of auricularis posterior EMG occurs concomitant with a tendency to facilitation of frontalis EMG (Stekelenburg & Van Boxtel, 2001). These considerations led us to the conclusion that, from an evolutionary viewpoint, the function of auricularis posterior inhibition during orienting can be conceived as prohibiting interference with pinna movements enhancing auditory input that are effected by the antagonistic auricularis anterior and superior muscles.

The unilateral facilitation of auricularis posterior EMG during lateral auditory stimulation can be understood as a vestigial response derived from a system of integrated directing responses of eyes, pinnae, and head toward external sources of visual,

auditory, or tactile stimulation (Middlebrooks & Knudsen, 1987; Stein & Clamann, 1981). These responses are controlled by a mechanism at the level of the superior colliculus that transduces sensory cues within different sensory modalities into adaptive motor responses producing nonselective tuning of the receptor organs toward stimuli of various sensory modalities, for example directing the eyes and pinnae toward both visual and auditory stimuli. In the cat, strong motor connections have been demonstrated between the superior colliculus and motoneurons in the facial nucleus innervating extrinsic ear muscles (Henkel & Edwards, 1978; Vidal, May, & Baker, 1988).

7.7 General discussion and concluding remarks

From the heart rate and skin conductance responses in Experiments 1 and 2, we can infer that orienting responses were successfully elicited by the novel auditory stimuli presented unexpectedly during the reading task. In agreement with our expectation, the orienting responses included significant respiratory and pericranial muscular components that showed coherency with the autonomic components. The stimuli induced an instantaneous slowing of respiration and a decrease in respiration depth. Sustained inhibition of EMG activity was consistently observed in masticatory and lower facial muscles (temporalis, mylohyoideus, and zygomaticus). The expected inhibition in orbicularis oculi was not found but this could be explained by the fact that the auditory stimuli were presented against a background EMG inhibition that was induced by the reading task. The expected inhibition in auricularis posterior was found under the condition that lateral eye or head movements toward the stimulus were absent. However, the inhibition turned into a facilitation when lateral directing responses toward the stimulus were made.

The currently observed cardiac, respiratory, and pericranial inhibitory responses are probably controlled by different pharmacological systems in the brain (Saiers, Richardson, & Campbell, 1989) but there is substantial evidence that they are centrally coordinated and integrated (see review by Stekelenburg & Van Boxtel, 2001). In our earlier study, we have shown that this integrated inhibitory response pattern is accompanied by a decrease in auditory threshold for low-frequency tones. The currently demonstrated emergence of these inhibitory responses as part of the orienting response is consistent with the hypothesis of Sokolov (1963) that the primary function of the generalized orienting response is a nonselective enhancement of the sensitivity of sensory modalities. The sensory function of the inhibitory response pattern does not seem limited to involuntary orienting to unexpected nonsignal stimuli. Inhibitory responses have also been observed during situations of voluntary attention to signal stimuli (Stekelenburg & Van Boxtel, 2001) or anticipation of signal stimuli (Van Boxtel et al., 1996), suggesting that increased sensory sensitivity is also a constituent of Sokolov's local orienting response.

Chapter 8

Summary and conclusions

8.1 Introduction

In this thesis the motor manifestations to the presentation of novel unexpected auditory stimuli were investigated. Such stimuli typically evoke an involuntary attention switch, called the orienting response (OR). The OR is defined as a complex of nonspecific behavioral and physiological responses to an unexpected sudden change in the immediate environment, leading to an increase in alertness and attention. The behavioral and physiological responses include interruption of ongoing activity, directing the sensory organs to the stimulus, heart rate deceleration, an increase in electrodermal activity, and EEG desynchronization. Sokolov (1960) developed a very influential theory explaining the origin of the OR. He suggested that each stimulus leaves a hypothetical trace or neuronal model in the central nervous system. The incoming stimulus is compared with the neuronal model of past stimulation. If there is a mismatch between the incoming stimulus and the neuronal model of previous stimulation, an OR is evoked. If the same stimulus is repeatedly presented, the mismatch between the neuronal model and the incoming stimulus decreases with the result that the attentive behaviors which the novel stimulus initially evoked, diminish in strength and ultimately disappear. This process is called habituation.

It is generally believed that the behavioral and physiological responses are evoked to enable closer perception of the novel stimulus. For this reason, the OR is called the "What-is-it? response." According to Sokolov (1969) the functional significance of the OR is to increase analyzer sensitivity, resulting in facilitation of the uptake, transmission, and analysis of environmental information. Others (e.g., Germana, 1968; Ruttkay-Nedecky, 1969) claimed, however, that the primary function of the OR is to prepare the individual for action in order to be able to better cope with the environment. In other words, the behavioral and physiological responses occurring during the OR are said to subserve behaviorally efficient adaptation to changes in the environment. According to these investigators, in response to OR-eliciting stimuli the individual is primarily concerned with the question "What has to be done?".

This difference in perspectives on the function of the OR has not yet been resolved. One of the reasons for this is that systematic investigation of changes in the motor system during the OR is still an underdeveloped field of research. The aim of the present research project was to explore the changes in motor activity elicited by the presentation of (novel) auditory stimuli. Stimulus related changes in motor activity were studied with regard to the functional significance of the OR. It was questioned whether changes in motor activity during the OR point to motor preparation that mobilizes the organism to cope with the changes in the environment. Alternatively, it was questioned whether it is possible to identify motor behavior subserving the hypothesized sensory function of the OR.

8.2 Does the OR facilitate motor output processes?

It was argued that if orienting increases the readiness for activity in the skeletal muscles, the OR would be accompanied by increased muscular activity. Increased muscle tone would cause the motor system to be brought closer to the motor action limit which in turn would result in faster responding. Chapter 5 studied whether during the OR there exists a period in which the motor system is facilitated. The changes in the motor system during the OR was examined by evoking spinal reflexes (Achilles tendon reflexes or T reflexes) after presentation of (novel) auditory stimuli. The amplitude of spinal reflexes reflects the number of alpha motoneurons that discharge or are subliminally activated. Spinal reflexes are a more sensitive measure compared to surface EMG (electromyographic) activity because reflex amplitudes also reflect subthreshold excitability changes within the motoneurons. It has repeatedly been demonstrated that auditory stimulus presentation induces a generalized facilitation in motor activity. This generalized facilitation is reflected in enhanced spinal reflex amplitudes from 50 ms to about 250 ms after auditory stimulus onset (Beale, 1971; Delwaide & Schepens, 1995; Liegeois-Chauvel et al., 1989; Rossignol & Melvill Jones, 1976; Rudell & Eberle, 1985; Scheirs & Brunia, 1982). Reflex facilitation is maximal at about 100 ms after stimulus onset.

Brunia and Boelhouwer (1988) advanced that this audiospinal facilitation is part of an alerting process possibly related to the OR. If audiospinal facilitation is indeed an OR-mediated effect, it should display the defining characteristics of the OR, including response decrement across repeated presentation of identical stimuli, recovery in response to a deviant stimulus, and dishabituation to the renewed presentation of the original stimulus. This was tested in two experiments using a so-called repetition-change paradigm. In this paradigm, a number of identical stimuli are presented, followed by a deviant stimulus and once more by the original (habituation) stimulus. In Experiment 1 of chapter 5, the habituation stimulus was loud (85 dB(A)) and the deviant stimulus soft (70 dB (A)) or vice versa. The habituation stimulus in Experiment 2 was a 70-dB(A) tone of 1000 Hz, the deviant stimulus was a 70-dB(A) tone of 500 Hz. In both experiments T reflexes were evoked at 100 ms after tone onset. In Experiment 1, T reflex amplitude decreased across identical stimuli, showed recovery only to the loud deviant, and dishabituated after both the intensity increase and decrease. Because spinal reflex amplitude is known to increase as a function of auditory stimulus intensity, the significant recovery to the intensity increase and the absence of recovery to the intensity decrease may have been the result of stimulus intensity per se. The activating effects of the intensity change may have obscured the effect of novelty – induced by the stimulus change – on T reflex amplitude. Therefore, in Experiment 2, the deviant stimulus consisted of a qualitatively different stimulus (change of pitch). Two variables were additionally introduced: interstimulus interval (ISI: 2.5 s vs. 7.5 s) and stimulus relevance (relevant vs. irrelevant). Participants had to give either a manual response in the stimulus-relevant condition or to perform a primary visual vigilance task in the stimulus-irrelevant condition. According to the OR theory, longer ISIs and relevant

stimuli should evoke stronger ORs and/or slower response decrement than shorter ISIs and irrelevant stimuli. In Experiment 2, in addition to T reflexes, event-related potentials (ERPs: N100 and P3) and the skin conductance response (SCR) were recorded as representatives of cerebral and autonomic indices of the OR, respectively. It was hypothesized that T reflex amplitude, SCR, and the (nonspecific component of) N100 were affected in a similar fashion by the experimental manipulations because the literature suggested that these response measures may be mediated by a common neural source, that is, the mesencephalic reticular formation (MRF) in response to (auditory) stimulation. Both T reflex amplitude, SCR, N100, and P3 rapidly decreased with repetition of identical stimuli. ISI and stimulus relevance differently affected the response amplitude and the rate of decrement of the different response measures. Stimuli with long ISIs evoked a larger N100 and P3 than stimuli with short ISIs. ISI did not affect T reflex amplitude. SCR in the short-ISI condition could not be examined because of overlapping responses elicited by subsequent stimuli which prevented the scoring of maximum skin conductance in any particular trial. Relevant stimuli evoked a larger N100 (at electrode position Cz) and P3 at all recorded electrode positions (F3, Fz, F3, T3, C3, Cz, C4, T4, and Pz) compared to irrelevant stimuli. SCR magnitude and T reflex amplitude were not affected by stimulus relevance. Stimulus relevance did not affect the rate of response decrement in any response system. The occurrence of recovery and dishabituation also differed for different response systems. Recovery was significant for SCR, P3, and T reflex amplitude, whereas recovery of N100 depended on specific combinations of ISI and stimulus relevance (short-ISI/stimulus-relevant condition and long-ISI/stimulus-irrelevant condition). Dishabituation was found for SCR and P3 (at electrode position Pz). The N100 showed dishabituation only with long ISIs. T reflex amplitude showed dishabituation in only one out of four conditions (short-ISI/stimulus-relevant condition).

Although we demonstrated that the short-latency audiospinal facilitation displayed (at least) two important defining characteristics of the OR, that is, response decrement and recovery to a change in pitch or to an intensity increase, the question is what the functional significance is of this response. It was argued that if an OR-evoking stimulus alerts the whole motor system to be ready for action, facilitation of the motor system should be prolonged for several hundreds of milliseconds, because it takes considerably longer than 100 ms to respond adequately to a change in the environment. Therefore, in Experiments 3 and 4, T reflexes were evoked at more delayed tone-reflex intervals (Experiment 3: 100, 200, and 300 ms; Experiment 4: 200, 300, 400, and 500 ms). Reflexes were evoked after each stimulus in an oddball paradigm wherein an infrequent deviant stimulus (1100 Hz) was interspersed in a homogeneous stimulus sequence (1000 Hz). In Experiments 3 and 4, stimulus relevance was varied as well. Participants were instructed either to ignore the stimulus by reading a book (stimulus-irrelevant condition) or to actively pay attention to the stimulus by counting the occurrence of the deviant tone (stimulus-relevant condition). Infrequent deviant stimuli

typically induce an event-related shift in brain activity called the mismatch negativity (MMN) irrespective of the subject's attention for the stimuli. When the stimulation is being paid attention to, infrequent deviant stimuli elicit a P3. Although the MMN and the P3 are functionally different responses, both are associated with the OR, that is, attention switching. As expected, a MMN was found in both conditions, whereas a P3 was only found in the stimulus-relevant condition

The question is whether T reflex amplitude to a deviant stimulus is enhanced at these prolonged tone-reflex intervals, compared to the standard stimulus. The results are ambiguous. In Experiment 3, stimulus deviance evoked enhanced T reflex amplitudes at 200 and 300 ms after tone onset, but not at 100 ms after tone onset. In Experiment 4, stimulus deviance had no effect on T reflex amplitude at any tone-reflex interval. As in Experiment 2, stimulus relevance had no significant influence on T reflex amplitude. Thus, no unequivocal evidence was found for the hypothesis that stimulus deviance – evoking a call for attention – also evokes a (prolonged) facilitation of the motor system.

The question was raised what the functional significance is of the audiogenic T reflex facilitation. Does it reflect an increase in readiness for activity in the skeletal muscles, improving response execution? The current results and the results of other studies suggest that the short-latency increase of excitability of motoneurons is a manifestation of another response, namely the startle response. The startle response is an involuntary generalized response to high intensity, auditory stimuli with short rise times. It consists of an eyeblink, a short-latency contraction of flexor muscles, and heart rate acceleration. The startle response reflects a functionally different mode of attention than the OR. It represents a disengagement from ongoing activity and rejection of environmental stimuli.

The first indication that the measured motor activity reflects a startle response is that like startle responses, spinal reflexes are evoked only by relatively loud auditory stimuli with short rise times. The OR on the other hand is supposed to be evoked by stimuli of low or moderate intensity in any modality. Second, the time course of the facilitation of the T reflex amplitude does not support the hypothesis that audiogenic reflex facilitation reflects an increased readiness for action. Although a significant short-latency facilitation of T reflex amplitude was found (Experiments 1 and 2), the second oddball study (Experiment 4) demonstrated that this audiospinal facilitation was not present at more delayed tone-reflex intervals (up to 500 ms). So, stimulus novelty has only a very short facilitatory effect on T reflex amplitude. The duration of this effect is probably too short to be functional in improving response execution. The motor facilitation has waned long before the time of response execution. The time course of the facilitation of the T reflex amplitude indicates a startle response rather than an OR because the time of maximal audiospinal facilitation matches the onset latency of the startle response, measured in the same muscle. To conclude, the short-latency discharge of motoneurons or the increase in excitability of the motoneurons induced by auditory stimulus presentation does not reflect a generalized motor preparation

toward anticipated muscular activity. Therefore, the current results did not support the hypothesis that the OR facilitates motor output processes.

8.3 Motor manifestations of the OR associated with its sensory function

In chapter 6 and 7 it was investigated whether motor manifestations of the OR might entail sensory facilitation as was originally proposed by Sokolov (1963). Sokolov claimed that the OR is directed to an aspecific enhancement of the sensitivity of sensory modalities. The focus was on two physiological response systems that have received little or no attention in the study of the OR so far: respiration and activity of pericranial muscles innervated by the trigeminal and facial nerves. Both response systems may have a functional role during stimulus intake. In several studies, it has been observed that during orienting breathing is partially inhibited, probably reducing disturbing respiratory sounds. Van Boxtel, Damen, and Brunia (1996) proposed a similar functional role of inhibition of pericranial muscle activity during auditory stimulus intake. They found that in anticipation to the presentation of a reaction signal in a forewarned reaction time task, activity of muscles in the lower part of the face and the masticatory apparatus (orbicularis oculi, zygomaticus, temporalis, masseter, and mylohyoideus) was gradually inhibited in anticipation of the auditory response stimulus. They hypothesized that inhibition of activity in these pericranial muscles might increase the perceptual sensitivity to external auditory stimuli. This was explained by a decrease of the internal auditory noise produced by these muscles themselves. Indirectly, pericranial inhibition might be expected to be accompanied by relaxation of middle ear muscles, producing lower auditory thresholds, especially for low-frequency sounds. Consequently, if the primary function of the OR would be to increase the sensitivity of the auditory system, we may predict inhibition of pericranial muscle activity and inhibition of respiratory activity during the course of the OR. Such an inhibitory response pattern might quiet down somatic noise that interferes with the detection and identification of the OR-eliciting stimulus.

In chapter 6, the hypothesis of Van Boxtel et al. (1996) was tested. That is, it was investigated whether inhibition of pericranial EMG and respiration during sensory intake processes improves auditory sensitivity. EMG activity was recorded from eight different pericranial muscles (frontalis, temporalis, corrugator supercilii, orbicularis oculi, zygomaticus major, orbicularis oris inferior, mylohyoideus, and auricularis posterior) during an auditory signal detection task. In addition to EMG and respiration, heart rate was recorded also because heart rate deceleration is considered to be a reliable index of the OR. Participants were required to perform a delayed motor response with their right index finger when a stimulus (1500 Hz, 4 s stimulus duration) was detected. Stimulus intensities varied between the threshold level and clearly audible suprathreshold levels (0, 2, 4, 8, 24, and 48 dB). It was expected that as signal intensity was lowered to the threshold level, increasing the difficulty of detection, pericranial EMG activity would be proportionally inhibited coinciding with increasing bradycardia and suppression of

respiration (i.e., suspension of inspiration and prolongation of the respiratory cycle) to raise the chance of detection. The results show that the mean EMG activity level in the temporalis, orbicularis oculi, zygomaticus, mylohyoideus, and auricularis posterior muscles during the presentation of detected stimuli decreased with decreasing stimulus intensity. EMG activity of the upper facial muscles (especially corrugator) increased progressively with decreasing stimulus intensity. The increase of activity of the corrugator might reflect increasing effortful attention to stimuli which are more difficult to detect. EMG activity of the lower facial and masticatory muscles decreased under the prestimulus baseline level for the four weakest stimulus intensities. Heart rate and respiratory activity showed a similar response as did the lower facial and masticatory muscles. Heart rate deceleration and slowing of respiration became stronger with decreasing stimulus intensities. Prestimulus baseline EMG activity of lower facial and masticatory muscles was significantly larger preceding undetected than preceding detected stimuli, suggesting that a relative higher background muscle level activity negatively affected auditory sensitivity. These results suggest that inhibition of breathing and muscle activity in the lower part of the face enhances auditory sensitivity. For upper facial muscles there was no relationship between baseline activity and stimulus detection. Auditory sensitivity is probably not affected by EMG activity of the upper facial muscles.

Two additional experiments were carried out to investigate more closely the causal relationship between the observed pericranial EMG responses and stimulus detection rates. Auditory threshold was assessed during steady, voluntary muscular contractions of varying strength that were maintained by means of visual EMG feedback. The effects of contraction of two representative pericranial muscles (corrugator and zygomaticus) and a small hand muscle (first dorsal interosseus) on auditory sensitivity were investigated. In the first experiment, the contraction level was 20% of maximal voluntary contraction level (EMG_{max}). In the second experiment, it was 50%, but because of the relatively fast fatigability of the first dorsal interosseus muscle, the contraction level of this muscle was maintained at 20%. Each participant was presented 100-Hz and 1500-Hz tones on separate days. The 100-Hz tone was included because negative effects of pericranial muscle contractions on auditory sensitivity was particularly expected for low-frequency sounds. Stimulus intensities were just under and just above the auditory threshold (–2, –1, 0, 1, 2, 3, 4, and 5 dB). Because the contraction level of 20% of EMG_{max} only had a small effect on the detection of the weak tones, only the results 50% experiment will be discussed here. Contraction of zygomaticus at 50% of EMG_{max}, had, compared to contraction of the corrugator or first dorsal interosseus, a negative effect on the auditory threshold (i.e., the percentage detected stimuli) for the 100-Hz tones but not for the 1500-Hz tones. The percentage of detected stimuli did not differ between contraction of corrugator and the first dorsal interosseus. The results of the experiments in chapter 6 confirm the existence of a causal relationship between lower facial and masticatory muscle activity and auditory sensitivity.

Chapter 6 suggests that inhibition of pericranial muscle activity, together with inhibition of respiration and heart rate, has a sensory functionality during *voluntary* attention to external stimuli. Chapter 7 explored whether these inhibitory responses are functional during *involuntary* attention to external stimuli. In other words, is the inhibitory response pattern an intrinsic component of the OR? Two experiments were carried out in which pericranial EMG activity, respiration, heart rate, and SCR during the OR were recorded. In the first experiment, a stimulation paradigm was used in which strong, nonhabituating ORs were expected. This was realized by the presentation of unexpected, weak auditory stimuli with a high degree of novelty and complexity. Participants were engaged in a primary task (reading a text) and were not informed about the presentation of the auditory stimuli. During this task, environmental sounds (e.g., human talk, animal sounds, and industrial sounds) were occasionally presented by a hidden loudspeaker located to the left of the participant. As expected, stimulus presentations elicited orienting responses as indicated by skin conductance increase and heart rate deceleration. Orienting responses were characterized by respiratory inhibition as can be inferred from a prolonged respiratory period indicating slowing of breathing and a reduced respiratory amplitude.

EMG activity of temporalis, zygomaticus, and mylohyoideus was significantly inhibited during stimulus presentation. The observed pattern of EMG responses confirmed the hypothesis that inhibition of EMG activity of masticatory and lower facial muscles during the OR subserves detection and identification of the auditory stimulus. Contrary to the expectation, EMG activity of orbicularis oculi was not inhibited but showed a transitory inhibition followed by a gradual increase during auditory stimulation. This unexpected finding was explained by taking into account the background EMG activity of this muscle during the reading task. The observations revealed that EMG activity of orbicularis oculi was inhibited during the reading task, suggesting that the increasing EMG activity during stimulus presentation reflected a state of progressive disinhibition and a return to the resting baseline level.

In Experiment 2 of chapter 7, it was investigated whether the inhibitory responses as found in Experiment 1 would habituate with repeated presentation of the same stimulus. A subset of seven different stimuli was taken from Experiment 1. Each stimulus was presented six times in succession, resulting in seven blocks of six identical stimuli. It was expected that the first presentation of a certain stimulus would evoke an OR that would habituate with repeated presentation. The OR was expected to recover at the first presentation of a novel stimulus. The obtained response scores were averaged across the presentations of the seven stimuli that occupied similar ordinal positions within the seven stimulation blocks. The response scores of the different physiological response systems all showed significant habituation, supporting the hypothesis that they constitute intrinsic components of the OR.

In both experiments, the EMG activity of the auricularis posterior muscle contrasted the findings in the first experiment of chapter 6. Whereas in the first

experiment of chapter 6, weak auditory stimuli induced significant inhibition of auricularis posterior EMG, novel stimuli in the experiments described in chapter 7 evoked enhanced EMG activity in this muscle on the ipsilateral side to the stimulus presentation (the soundspeaker was directed perpendicular to the left ear). It was suspected that this was not an effect of stimulation side but related to head and/or eye rotations to the source of the stimulation assuming that participants (slightly) rotated their head and eyes toward the source of the stimulation. The unilateral EMG response may have been induced by two effects. First, the electrodes of the auricularis posterior muscle might have picked up activity of the muscle which is responsible for ipsilateral head rotation (splenius capitis). Second, lateral eye movements may have caused the unilateral activation of the auricularis posterior, an effect belonging to the oculo-auricular phenomenon.

Two additional control experiments were conducted to disentangle the effects of stimulation side on the one hand and head and eye rotation on the other hand on the EMG response of the auricularis posterior muscle. Participants deliberately performed ipsilateral or contralateral rotation of the head or eyes during unilateral stimulus presentation. It was examined whether the unilateral facilitation of auricularis posterior EMG could be replicated and whether ipsilateral stimulus presentation or ipsilateral head or eye rotation were crucial for bringing about this EMG response. The results suggest that the unilateral facilitation of auricularis posterior EMG observed in Experiments 1 and 2 of chapter 7 was not a primary effect of ipsilateral stimulus presentation. Instead, lateral rotation of both head and eyes appears to facilitate the ipsilateral auricularis posterior EMG. In the third condition of Experiment 3, the participants did not perform head rotations but kept their head and eyes fixed in a frontal position. In this condition, unilateral auditory stimulation induced a significant inhibition of EMG activity in the auricularis posterior muscle. This result, in conjunction with the results of chapter 6, suggests that inhibition of the auricularis posterior EMG is a vestigial response allowing the erection of the pinna and facilitating auditory input.

In summary, the experiments described in chapter 6 and 7 showed that suppression of breathing and inhibition of pericranial muscle activity during unexpected, novel, weak auditory stimuli seems efficacious for the detection and discrimination of weak auditory stimuli. These inhibitory responses appear to be intrinsic response components of the OR.

8.4 Final conclusions

(1) Auditory stimuli of moderate or high intensity evoke a short-latency enhancement of spinal reflex amplitude of short duration. This motor response is a reflection of the startle response. It does not reflect a generalized motor preparation toward anticipated action.

(2) There is a causal relationship between activity of masticatory and lower facial muscles and auditory sensitivity. Increased activity of these muscles negatively affects

auditory sensitivity. Activity of the upper facial muscles has no direct influence on auditory sensitivity.

(3) Voluntary attention to weak auditory stimuli and involuntary orienting to novel, nonsignal auditory stimuli are accompanied by inhibition of masticatory and lower facial muscle activity and inhibition of respiratory activity. These responses quiet down somatic noise and facilitate middle ear transmission of low-frequency sounds, thereby improving the detection and identification of the stimulus.

(4) Summarizing, involuntary orienting to nonsignal, auditory stimuli elicits a somatic and autonomic response pattern with a sensory utility. We found no convincing evidence that the primary function of the OR is to prepare the organism for motor action. On the contrary, the results of the current study confirm the hypothesis of Sokolov that the primary function of the OR is to increase analyzer sensitivity.

Samenvatting

Dit proefschrift bestudeert het gedrag van mensen dat wordt opgeroepen door een nieuwe, onverwachte prikkel of stimulus uit de omgeving, bijvoorbeeld de lach van de bonte specht tijdens een boswandeling. Een gebeurtenis als deze bewerkstelligt dat de aandacht automatisch wordt gericht op de nieuwe stimulus. Zo'n aandachtsverschuiving gaat gepaard met bepaalde gedragsmatige en fysiologische reacties die tezamen de Oriëntatie Reactie (OR) worden genoemd. Voorbeelden van gedragsmatige reacties zijn: het stoppen van het gedrag dat aan de gang was (bijvoorbeeld je stopt met wandelen) en het richten van ogen en hoofd naar de stimulus (om te luisteren naar de bron van het geluid). Fysiologische reacties bestaan uit bijvoorbeeld vertraging van de hartslag, toename in huidgeleiding (reactie van de zweetklieren) en veranderingen in hersenactiviteit.

De alom heersende gedachte, vooral ingegeven door Sokolov (1963), is dat deze reacties dienen om de verwerking van de stimulus te optimaliseren. De OR wordt daarom omschreven als de "wat-is-het? reactie." Anderen (o.a. Germana, 1968) zijn daarentegen van mening dat de primaire functie van de OR is om het individu voor te bereiden op een mogelijke actie zodat er adequaat kan worden gereageerd op de verandering in de omgeving. Volgens dit standpunt reageert het individu op de nieuwe stimulus met de vraag "wat moet er gebeuren?" Kortom, volgens de eerste opvatting behelst de OR optimalisatie van stimulus input gerelateerde processen terwijl volgens de tweede opvatting motorische output processen worden gefaciliteerd.

Tot nu toe is er nog geen definitief uitsluitstel over welke van beide opvattingen het meest plausibel is. Eén van de redenen hiervoor is dat onderzoek naar veranderingen in het motorische systeem tijdens de OR schaars is. Het doel van dit proefschrift was om op systematische wijze de veranderingen in motorische activiteit ten gevolge van nieuwe onverwachte auditieve stimuli te onderzoeken. Daartoe werden twee vragen gesteld. Duiden veranderingen in motorische activiteit op motorische preparatie tijdens de OR (de tweede opvatting)? Of zijn er motorische respons patronen aan te wijzen die de sensorische functie van de OR ondersteunen (de eerste opvatting)? Deze samenvatting geeft de belangrijkste bevindingen weer.

Is er motorische preparatie tijdens de OR?

In het eerste data-hoofdstuk (hoofdstuk 5) worden de resultaten van vier experimenten beschreven om een antwoord te kunnen geven op de vraag of er sprake is van activering of facilitatie van het motorische systeem tijdens de OR. Dit werd onderzocht door na presentatie van auditieve stimuli op verschillende tijdstippen achillespeesreflexen op te wekken. Achillespeesreflexen (tendon reflexes of T reflexen) worden opgewekt in de kuitspieren door een tikje te geven tegen de achillespees. De amplitude van de T reflex weerspiegelt de prikkelbaarheid van motorische structuren in het ruggenmerg. Het is een maat voor motorische activering. In eerdere experimenten is gevonden dat de presenta-

tie van een auditieve stimulus direct voorafgaand aan het tikje op de achillespees leidt tot een toename van de amplitude van de T reflex. Dit wordt audiospinale facilitatie genoemd. Deze is het grootst wanneer de T reflex op 100 ms na de stimulus wordt opgewekt.

De vraag is nu of audiospinale facilitatie een maatstaf is voor toegenomen motorische preparatie gedurende de OR. Wanneer dat zo is, zou men verwachten dat de facilitatie voldoet aan de eigenschappen van de OR. Dat wil zeggen, de facilitatie neemt in sterkte af wanneer dezelfde stimulus herhaaldelijk wordt aangeboden (habituatie) en verschijnt weer als er een afwijkende (deviante) stimulus volgt (herstel). Wanneer de oorspronkelijke stimulus daarna opnieuw wordt aangeboden, is de reactie hierop sterker dan voor het herstel (dishabituatie). Verschillende experimenten zijn uitgevoerd om te onderzoeken of de amplitude van T reflexen habituatie vertoont en gevoelig is voor stimulusdeviantie. Hierbij werd gebruik gemaakt van experimentele designs die eerder betrouwbare fysiologische indices voor de OR hebben opgeleverd.

Uit de resultaten van de eerste twee experimenten blijkt dat audiospinale facilitatie op 100 ms na stimulusaanvang op belangrijke punten voldoet aan de kenmerken van de OR. Echter, omdat het veel langer duurt dan 100 ms om adequaat op een verandering in de omgeving te reageren, zou het motorische systeem langer (zeker een paar honderd milliseconden) gefaciliteerd moeten zijn. Daarom werden in twee vervolgexperimenten T reflexen opgeroepen op latere tijdstippen, tot maximaal 500 ms, na deviante stimuli. Daaruit bleek dat er zich op langere toon-reflex intervallen (de tijd tussen de toon en het opwekken van de T reflex) geen betrouwbare facilitatie meer voordeed.

Op basis van de uitkomsten van deze experimenten kan geconcludeerd worden dat T reflex facilitatie geen uitdrukking is van een algehele motorische preparatie in reactie op een nieuwe onverwachte stimulus. De audiospinale facilitatie duurt te kort om functioneel te kunnen zijn voor respons executie, dat wil zeggen het daadwerkelijk reageren. De motorische facilitatie is weggeëbd voordat er een mogelijke reactie kan worden gegeven op de verandering in de omgeving. Het tijdsverloop van de facilitatie van de T reflex over de toon-reflex intervallen samen met de afhankelijkheid van audiospinale facilitatie van stimulusintensiteit en de stijgtijd daarvan (hoe harder de toon en hoe sneller de geluidssterkte aan het begin van de toon oploopt des te groter de amplitude van de reflex) suggereren dat de motor respons niet zozeer aan de OR is gerelateerd maar aan een andere reactie, namelijk de "startle-response" (d.w.z. een schrikreactie).

Pericraniale motorische componenten van de OR

Hoofdstukken 6 en 7 richten zich op de vraag of tijdens de OR motorische activiteit plaatsvindt die de sensorische functie van de OR ondersteunt. Volgens Sokolov (1963) is de functie van de OR de sensorische gevoeligheid voor externe stimuli te verhogen. In dit proefschrift wordt gesteld dat de motorische activiteit van bepaalde pericraniale spieren (gelaatsspieren) een functionele rol heeft tijdens de OR op onverwachte auditieve stimuli. Van Boxtel, Damen en Brunia (1996) beweerden dat inhibitie (ontspanning) van spieren in het onderste gedeelte van het gelaat en van de kaakspieren de sen-

sorische gevoeligheid voor auditieve stimuli bevordert. Dit wordt verklaard door middel van twee effecten. Ten eerste, deze spieren produceren een hoorbaar achtergrondgeruis dat via botgeleiding naar het oor wordt getransporteerd. Door inhibitie van spieractiviteit in deze gelaatsspieren zou de interne auditieve ruis afnemen en daarmee de auditieve gevoeligheid toenemen. Ten tweede kan ook op een meer indirecte manier pericraniale inhibitie de auditieve gevoeligheid beïnvloeden. Inhibitie van de spieractiviteit in de onderste helft van het gelaat en van de kaakspieren kan vergezeld gaan met ontspanning van middenoorspieren. Dit laatste zou resulteren in een lagere auditieve gehoordrempel, met name voor laagfrequente geluiden. Met andere woorden, door deze twee effecten kunnen (zachte) geluiden beter worden waargenomen. Als wordt aangenomen dat de primaire functie van de OR is om de gevoeligheid van de sensorische systemen te verhogen, is de verwachting dat de OR wordt gekenmerkt door inhibitie van bovengenoemde spieren.

Een ander systeem dat mogelijkerwijs een functionele rol heeft tijdens de OR is ademhaling. Ademhaling gaat gepaard met hoorbare geluiden die de auditieve gevoeligheid negatief kunnen beïnvloeden. Daarom wordt verwacht dat tijdens de OR de ademhaling gedeeltelijk wordt ingehouden of onderdrukt.

In hoofdstuk 6 wordt eerst onderzocht of er daadwerkelijk een relatie bestaat tussen enerzijds gelaatsspier- en ademhalingsactiviteit en anderzijds auditieve gevoeligheid. Ademhaling en spieractiviteit in diverse gelaatsspieren werden gemeten gedurende een auditieve signaal-detectie taak waarin proefpersonen tonen van verschillende intensiteiten moesten detecteren (van 0 dB, d.w.z. de gehoordrempel, tot 48 dB). De verwachting was dat naarmate de tonen moeilijker hoorbaar zijn de ademhaling en de spieractiviteit in het onderste gedeelte van het gelaat en van de kaakspieren meer zullen worden geïnhibeerd om de kans op detectie van de tonen te verhogen.

Er werden drie aanwijzingen gevonden dat er een relatie bestaat tussen gelaatsspieractiviteit en auditieve gevoeligheid.

Ten eerste, zoals verwacht was de inhibitie van spieractiviteit en van de ademhaling (langere ademhalingscyclus en onderdrukking van inademing) sterker naarmate de tonen steeds zachter klonken.

Ten tweede, het detecteren van zachte tonen was afhankelijk van "ongoing" spieractiviteit. Zeer zachte tonen werden de ene keer wel en de andere keer niet gedetecteerd. Volgens de theorie van Van Boxtel et al. (1996) kan dit worden verklaard doordat een relatief hoog niveau van spontane spieractiviteit – net voordat de toon klinkt – de gehoordrempel verhoogt, dat wil zeggen dat de kans om de tonen te detecteren, afneemt. Dit is precies wat werd gevonden. De spieractiviteit in het onderste gedeelte van het gelaat en van de kaakspieren – gemeten onmiddellijk voor stimulusaanvang – was hoger voor de niet gedetecteerde tonen dan voor de gedetecteerde tonen. Dit suggereert dat een relatief hoog niveau van "ongoing" spieractiviteit de auditieve gevoeligheid negatief beïnvloedt.

Ten derde, in een vervolgexperiment werd de relatie tussen gelaatsspieractiviteit en

auditieve gevoeligheid op een meer directe manier onderzocht. Er werd getest of vrijwillige constante aanspanning van bepaalde gelaatsspieren de auditieve gevoeligheid inderdaad negatief beïnvloedt. Gedurende een auditieve signaal-detectie taak moesten proefpersonen ofwel een spier in het onderste gedeelte van het gelaat (wangspier) aanspannen, of een spier in het bovenste gedeelte van het gelaat (fronsspier), of een kleine handspier (tussen duim en wijsvinger). Zoals verwacht resulteerde de contractie van de wangspier in een hogere auditieve drempel vergeleken met de fronsspier en de handspier.

De resultaten van hoofdstuk 6 bevestigen dat er een causale relatie bestaat tussen spieractiviteit in de onderste helft van het gelaat en van de kaakspieren enerzijds en de auditieve gevoeligheid anderzijds.

Aangenomen dat de OR een sensorische functie heeft, is de verwachting dat er inhibitie van de spieractiviteit en ademhaling zal optreden op auditieve stimuli die een OR oproepen. In twee experimenten, beschreven in hoofdstuk 7, kregen proefpersonen daarom onverwachte geluiden te horen terwijl ze een andere taak uitvoerden, namelijk het lezen van een tekst waarvoor ze al hun aandacht nodig hadden. Hiervoor werden geluiden gebruikt die (in theorie) een sterke OR oproepen: nieuwe, onverwachte, complexe, auditieve stimuli zoals omgevingsgeluiden, humane spraak, diergeluiden en muziekfragmenten, van lage intensiteit (± 30 dB). In het eerste experiment kregen de proefpersonen steeds verschillende geluiden te horen. In het tweede experiment werden herhalingen van dezelfde geluiden aangeboden. Daarmee werd habituatie van de OR onderzocht. Zoals verwacht, riepen de stimuli inhibitie van de ademhaling op. Tijdens de OR werd de ademhaling trager en oppervlakkiger. De OR werd tevens gekenmerkt door inhibitie van diverse spieren in het onderste gedeelte van het gelaat. Beide inhibitoire reacties vertoonden habituatie. Met andere woorden, de inhibitie van ademhalings- en gelaatsspieractiviteit, opgeroepen door een nieuwe onverwachte stimulus, nam af wanneer dezelfde stimulus herhaaldelijk werd aangeboden. Deze habituatie was vergelijkbaar met de habituatie van betrouwbare indices van de OR (huidgeleiding en vertraging van de hartslag) die gelijktijdig werden gemeten. In hoofdstuk 7 wordt geopperd dat de onderdrukking van de ademhaling en inhibitie van spieractiviteit in het onderste gedeelte van het gelaat en van de kaakspieren intrinsieke componenten van de OR (op auditieve stimuli) vormen met als mogelijke functie om de somatische geluiden die kunnen interfereren met de detectie en identificatie van nieuwe stimuli te onderdrukken.

Concluderend kan worden gesteld dat nieuwe onverwachte auditieve stimuli lichamelijke reacties oproepen die een sensorische functie hebben. In dit proefschrift is geen overtuigend bewijs gevonden voor de stelling dat de OR gepaard gaat met preparatie op motorische actie. Integendeel, de gevonden resultaten bevestigen de hypothese van Sokolov dat de primaire functie van de OR is om de verwerking van de nieuwe stimulus te optimaliseren.

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When someone is confronted with a sudden unexpected change in the environment such as a birdcall, attention is automatically shifted to the novel stimulus. This involuntary attention switch is called the orienting response. The aim of the thesis was to explore the changes in motor activity during the orienting response. It was investigated whether the observed motor behavior indicates increased readiness for possible action in response to the changed situation. Alternatively, it was questioned whether we could identify changes in motor activity with the function of improving the detection, identification, and processing of the novel stimulus. The results suggest that the presentation of novel auditory stimuli does not induce a long lasting facilitation of the motor system, invalidating the hypothesized preparatory function of the OR. Involuntary attention to novel auditory stimuli is accompanied by relaxation of the muscles in the lower part of the face which increases auditory sensitivity. Our results confirm the hypothesis, originally proposed by Sokolov, that the primary function of the OR is to increase analyzer sensitivity.

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