Emotional Modulation of Motor Memory Formation

Emotionale Modulation des Motorischen Gedächtnises

Doctoral thesis for a doctoral degree
at the Graduate School of Life Sciences,
Julius-Maximilians-Universität Würzburg,
Section Neuroscience

submitted by
Cigdem Önal-Hartmann
from
Eskisehir/Türkiye

Würzburg 2011

Submitted on:

Members of the Promotionskomitee:
Chairperson: Prof. Dr. U. Holzgrabe
Primary Supervisor: Prof. Dr. J. Claßen
Supervisor (Second): Prof. Dr. P. Pauli
Supervisor (Third): Prof. Dr. A. J. Fallgatter

Date of Public Defence:
Date of receipt of Certificates:

Affidavit

(Eidesstattliche Erklärung)

I hereby declare that my thesis entitled “Emotional modulation of motor memory formation” is the result of my own work. I did not receive any help or support from commercial consultants. All sources and/or material applied are listed and specified in the thesis.

Furthermore, I verify that this thesis has not yet been submitted as part of another examination process neither in identical nor in similar form.

Würzburg 2011 Cigdem Önal-Hartmann

Acknowledgements

First of all, I would like to thank the primary supervisor of my thesis Prof. Dr. Joseph Claßen for his help in all aspects of my study. In addition I want to thank especially Prof. Dr. Paul Pauli, Prof. Dr. Onur Güntürkün and Prof. Dr. Andreas Jochen Fallgatter for advice and encouragement.

I am also thankful to my friends Dr. Mirta Fiorio, Dr. Reinhard Gentner, Dr. Marta Andreatta, Dr. Sarah Louise Nietzer and Dr. Robert Kordts-Freudinger for any comments, suggestions and support.

Finally I wish to thank all the subjects for their participation and patience in experiments.

Table of Contents

Summary **6**

Zusammenfassung **8**

General Introduction **11**

Definition of Emotion **12**

Methods to induce Emotions **14**

Memory **17**

Motor Skill Memory **17**

Explicit Memory and Emotion **18**

Motor Memory and Emotion **20**

Experiment 1 - ***The influence of emotion on encoding of a motor skill memory***

- **Introduction** **22**
- **Methods** **24**
- **Results** **27**
- **Discussion** **29**

Experiment 2 - ***Emotion and the consolidation of sequence learning in humans***

- **Introduction** **32**
- **Methods** **34**
- **Results** **41**
- **Discussion** **49**

Experiment 3 - ***The motor side of emotions: Investigating the relationship between hemispheres, motor reactions and emotional stimuli***

- **Introduction** **56**
- **Methods** **59**
- **Results** **62**
- **Discussion** **64**

General Discussion **71**

References **75**

Appendix **96**

Summary

Background: There is extensive evidence that explicit memory, which involves conscious recall of encoded information, can be modulated by emotions; emotions may influence encoding, consolidation or retrieval of information. However, less is known about the modulatory effects of emotions on procedural processes like motor memory, which do not depend upon conscious recall and are instead demonstrated through changes in behaviour.

Experiment 1: The goal of the first experiment was to examine the influence of emotions on motor learning. Four groups of subjects completed a motor learning task performing brisk isometric abductions with their thumb. While performing the motor task, the subjects heard emotional sounds varying in arousal and valence: (1) valence negative / arousal low (V-/A-), (2) valence negative / arousal high (V-/A+), (3) valence positive / arousal low (V+/A-), and (4) valence positive / arousal high (V+/A+). Descriptive analysis of the complete data set showed best performances for motor learning in the V-/A- condition, but the differences between the conditions did not reach significance. Results suggest that the interaction between valence and arousal may modulate motor encoding processes. Since limitations of the study cannot be ruled out, future studies with different emotional stimuli have to test the assumption that exposure to low arousing negative stimuli during encoding has a facilitating effect on short term motor memory.

Experiment 2: The purpose of the second experiment was to investigate the effects of emotional interference on consolidation of sequential learning. In different sessions, 6 groups of subjects were initially trained on a serial reaction time task (SRTT). To modulate consolidation of the newly learned skill, subjects were exposed, after the training, to 1 of 3 (positive, negative or neutral) different classes of emotional stimuli which consisted of a set of emotional pictures combined with congruent emotional musical pieces or neutral sound. Emotional intervention for each subject group was done in 2 different time intervals (either directly after the training session, or 6 h later). After a 72 h post-training interval, each group

was retested on the SRTT. Re-test performance was evaluated in terms of response times and accuracy during performance of the target sequence. Emotional intervention did not influence either response times or accuracy of re-testing SRTT task performance. However, explicit awareness of sequence knowledge was enhanced by arousing negative stimuli applied at 0 h after training. These findings suggest that consolidation of explicit aspects of procedural learning may be more responsive toward emotional interference than are implicit aspects. Consolidation of different domains of skill acquisition may be governed by different mechanisms. Since skill performance did not correlate with explicit awareness we suggest that implicit and explicit modes of SRTT performance are not complementary.

Experiment 3: The aim of the third experiment was to analyze if the left hemisphere preferentially controls flexion responses towards positive stimuli, while the right hemisphere is specialized towards extensor responses to negative pictures. To this end, right-handed subjects had to pull or push a joystick subsequent to seeing a positive or a negative stimulus in their left or right hemifield. Flexion responses were faster for positive stimuli, while negative stimuli were associated with faster extensions responses. Overall, performance was fastest when emotional stimuli were presented to the left visual hemifield. This right hemisphere superiority was especially clear for negative stimuli, while reaction times towards positive pictures showed no hemispheric difference. We did not find any interaction between hemifield and response type. Neither was there a triple interaction between valence, hemifield and response type. In our experimental context the interaction between valence and hemifield seems to be stronger than the interaction between valence and motor behaviour. From these results we suppose that under certain conditions a hierarchy scaling of the asymmetry patterns prevails, which might mask any other existing asymmetries.

Zusammenfassung

Hintergründe: Wie eine Vielzahl von Studien belegt, kann das explizite Gedächtnis, das die bewusste Erinnerung an enkodierte Informationen beinhaltet, durch Emotionen beeinflusst werden, und zwar über den Einfluss auf verschiedene Verarbeitungsebenen (Enkodierung, Konsolidierung, Abruf usw.). Bisher wenig untersucht ist, ob und wie Emotionen Vorgänge der motorischen Gedächtnisbildung, die nicht auf bewusster Erinnerung beruhen und sich stattdessen durch Veränderungen im Verhalten darstellen, modulieren.

Experiment 1: Das Ziel des ersten Experimentes war es, den Einfluss von Emotionen auf motorisches Lernen zu untersuchen. Vier Gruppen von Probanden mussten in einer motorischen Lernaufgabe schnelle, seitliche Bewegungen mit dem Daumen ausführen. Während dieser Aufgabe hörten die Probanden emotionale Klänge, die in Valenz und Arousal variierten: 1. Valenz negativ/ Arousal niedrig (V-/A-), 2. Valenz negativ/ Arousal hoch (V-/A+), 3. Valenz positiv/ Arousal niedrig (V+/A-), 4. Valenz positiv/ Arousal hoch (V+/A+). Die deskriptive Analyse aller Daten sprach für beste Ergebnisse für das motorische Lernen in der Bedingung V-/A-, aber die Unterschiede zwischen den Bedingungen waren nicht signifikant. Die Interaktion zwischen Valenz und Arousal emotionaler Töne scheint demnach motorische Enkodierungsprozesse zu modulieren, jedoch müssen zukünftige Studien mit unterschiedlichen emotionalen Stimuli die Annahme weiter untersuchen, dass negative Stimuli mit niedrigem Arousal während der Enkodierung einen fördernden Effekt auf das motorische Kurzzeitgedächtnis haben.

Experiment 2: Die Absicht des zweiten Experimentes war es, die Auswirkungen emotionaler Interferenzen auf die Konsolidierung beim Sequenzlernen zu untersuchen. Sechs Gruppen von Probanden trainierten zuerst in getrennten Sitzungen eine SRTT-Aufgabe (serial reaction time task). Um die Konsolidierung der neu erlernten Fertigkeit zu modulieren, wurden die Probanden nach dem Training einer von drei unterschiedlichen Klassen emotionaler Stimuli (positiv, negativ oder neutral) ausgesetzt. Diese bestanden aus einem Set emotionaler Bilder,

die mit emotional kongruenten Musikstücken oder neutralen Klängen kombiniert waren. Bei den Probandengruppen wurde die emotionale Interferenz nach zwei unterschiedlichen Zeitintervallen realisiert, entweder direkt nach der Trainingssitzung oder sechs Stunden später. 72 Stunden nach der Trainingssitzung wurde jede Gruppe erneut mit der SRTT-Aufgabe getestet. Die Leistung in diesem Nachtest wurde mittels Reaktionszeit und Genauigkeit bei der Ausführung der Zielsequenz analysiert. Die emotionale Interferenz beeinflusste weder die Nachtestergebnisse für die Reaktionszeit noch die für die Genauigkeit. Allerdings konnte eine Steigerung der expliziten Sequenzerkennung durch erregende negative Stimuli festgestellt werden, wenn diese direkt nach der ersten Trainingseinheit (0h) dargeboten wurden. Diese Ergebnisse lassen vermuten, dass die Konsolidierung der expliziten Aspekte prozeduralen Lernens in einer stärkeren Wechselwirkung mit emotionalen Interferenzen stehen könnte als die der impliziten Aspekte. Die Konsolidierung unterschiedlicher Ebenen des Fertigkeitserwerbs könnte demnach von unterschiedlichen Mechanismen gesteuert werden. Da Performanz und explizites Sequenzerkennen nicht korrelierten, vermuten wir, dass implizite und explizite Modalitäten bei der Durchführung der SRTT-Aufgabe nicht komplementär sind.

Experiment 3: Es sollte untersucht werden, ob es eine Präferenz der linken Gehirnhemisphäre bei der Kontrolle von Flexionsreaktionen auf positive Stimuli gibt und der rechten Hemisphäre bei der Kontrolle von Extensionsreaktionen auf negative Stimuli. Zu diesem Zweck sollten rechtshändige Probanden einen Joystick zu sich ziehen oder von sich weg drücken, nachdem sie einen positiven oder negativen Stimulus in ihrem linken oder rechten Gesichtsfeld gesehen hatten. Die Flexionsreaktionen waren bei positiven Stimuli schneller, Extensionsreaktion hingegen bei negativen Stimuli. Insgesamt war die Performanz am schnellsten, wenn die emotionalen Stimuli im linken Gesichtsfeld präsentiert wurden. Dieser Vorrang der rechten Gehirnhemisphäre war besonders deutlich für negative Stimuli, wohingegen die Reaktionszeiten auf positive Bilder keine hemisphärische Differenzierung

zeigten. Wir konnten keine Interaktion zwischen Gesichtsfeld und Reaktionstyp belegen, auch fand sich keine Dreifachinteraktion zwischen Valenz, Gesichtsfeld und Reaktionstyp. In unserem experimentellen Kontext scheint die Interaktion zwischen Valenz und Gesichtsfeld stärker zu sein als die Interaktion zwischen Valenz und motorischem Verhalten. Auf Grund dieser Ergebnisse vermuten wir, dass unter gewissen Bedingungen eine Hierarchisierung der asymmetrischen Muster Vorrang hat, die möglicherweise andere vorhandene Asymmetrien maskieren könnte.

General Introduction

Each second that we are awake we find ourselves in a particular emotional condition. Even if we are often not aware of it: human existence always implies being in an emotional condition. What we feel affects our cognitive processes and our behaviour. We are, for instance, much better at remembering events that are linked to strong emotions, e.g. our happiest birthday, an accident, etc. Emotions even manifest themselves physically when someone annoyed jumps up from a chair, seems paralysed in mourning or pushes his hands out in horror. Good actors and cartoonists have recourse to the tight relationship between emotion and motion for their work when depicting the emotional state of their characters, often by a single, typical motion.

If, as we experience every day, emotions affect our motor behaviour to such a degree, are they also relevant to the learning and memory of motor processes? Would somebody learn faster how to steer a car and how to shift gears etc., if their co-driver were a person that would make him/her, happy or if it were someone who would permanently annoy him/her? Could someone for example learn the complicated finger movements inherent in the playing of a piano fugue faster, and keep these in memory better, if he has experienced something prior to learning which has rendered him happy or made him composed, or if he experienced something that has upset him?

The gamut of scientific questions that results from such deliberation is enormous. If we wish to make them accessible to experimental research, it is necessary to narrow them down to a few very specific aspects. The documented understanding of individual parts ought to help deepen the understanding of the whole – at least that is what we are hoping for.

This dissertation deals with the question of how emotions may affect motor memory processes. For this purpose we have developed, and conducted, several experiments on special sub domains. Before defining the goals and the in-and-outs of these experiments any closer,

we subsequently give some basic thought to what emotion is and how emotion induction can be implemented within an experimental context. We shall elaborate on the nature of memory and motor skill memory and then proceed to observe the outcome of important studies about emotional effects on memory processes, particularly on explicit memory. Finally we shall examine previous studies destined to explore the relationship between emotion and motor learning processes.

Definition of Emotion

"Everyone knows what emotion is, until asked to give a definition. Then it seems that no one knows" (Fehr&Russell, 1984). Emotional behaviours with a functional value, both in communication and in increasing the individual's chances of survival, have evolved across species (Darwin, 1872). The way how we express emotions is innate and inherited. For example, to express the feeling of anger we flash our teeth in the same way as our prehistoric ancestors did in a fight, or we shrug our shoulders to indicate indifference or resignation.

At the end of 19th century the James-Lange-theory (James, 1884; Lange, 1887) tried to explain emotion as a deduction from bodily states. Environmental stimulation provokes reactions of the autonomic nervous system like accelerated heart beat or a change of muscular tension. Experiencing these bodily changes we deduce our emotions from them. William James summarized: "My theory (…) is that the bodily changes follow directly the perception of the exciting fact, and that our feeling of the same changes as they occur is the emotion" (James, 1890). In other words, we feel happy because we laugh. In contrast to the James-Lange theory, which proposes a sequence of events, the Cannon-Bard Theory of Emotion (Bard, 1934; Cannon, 1927) suggests that recognition of subjective emotions and physiological changes occurs simultaneously and independently. Emotions can be experienced even if physiological changes cannot be sensed; an appropriative activation of the

thalamus is the sufficient condition for feeling an emotion. That is why we don't have to laugh to feel happy.

Recent research approaches like the somatic-marker hypothesis (Damasio, 1996) suggest that emotional processes can guide behaviours, in particular decision-making. Damasio's patient, Elliot, developed a brain tumour that damaged his prefrontal cortex. While his intelligence remained intact, his ability to make rational decisions was severely impaired, because his emotions could no longer be engaged in the process (Damasio, 1994). Cognitive appraisal theories of emotion suggest that our emotions are determined by the cognitive evaluation or appraisal of an event that is of personal relevance to us. Our appraisal of the potential consequences of an event determines the emotion we feel (Frijda, 1986; Scherer, 2001).

Since Darwin's theory on the evolutionary basis of emotional behaviours, it has been proposed to define a set of basic emotions. Ekman and Friesen (1969, 1971) examined emotional facial expressions across cultures. They suggested that the facial behaviours of anger, disgust, fear, joy, sadness and surprise represent basic emotions since they are judged to be of the same emotion, regardless of the observer's culture. Basic emotions can easily be classified along dimensions such as positive or negative (Cacioppo & Berntson, 1994), pleasant or unpleasant (Lang, Bradley, & Cuthbert, 1990), appetitive or aversive (Dickinson & Dearing, 1979), calm or excited (Osgood, Suci, & Tannenbaum, 1957).

Instead of defining dimensions based on the subjective experience of the emotion, some dimensional theorists have depicted emotions along the action pattern which the emotions prepare (action tendencies), such as "approach and withdrawal". According to the motivational approach-withdrawal hypothesis, stimuli that promote survival (e.g. food) elicit behaviour towards the stimulus, whereas those that are regarded as threatening (e.g. predator) lead to an individual behaviour away from the stimulus (Demaree, Everhart, Youngstrom, & Harrison, 2005). In this context, positive emotions can be linked to approach behaviours, and

avoidance behaviours to negative emotions. However, there are exceptions for this correspondence. Anger for example is considered an unpleasant emotion, but anger-evoking stimuli may drive us to fight or flight, in other words to approach or to avoid (Carver & Harmon-Jones, 2009).

It has become evident that the ostensibly small word "emotion" denotes a multifaceted phenomenon. As our central question is not about emotions per se, a comprehensive depiction would be beyond the scope of this paper. We therefore restrict ourselves and highlight once again its complexity, and the aspects we consider to be relevant, by quoting a "working definition" by Scherer (2000): emotions are "episodes of coordinated changes in several components (including at least neuro-physiological activation, motor expression, and subjective feelings but possibly also action tendencies as well as cognitive processes) in response to external and internal events of major significance to the organism".

Methods to Induce Emotions

To study emotions in laboratory settings we need stimuli that reliably induce cognitive, emotional and physiological reactions. Those reactions have to vary systematically over the range of expressed emotions (Bradley & Lang, 2000a). Today's most common method in emotion research can already to some extent be found in Darwin: photographs with emotional contents are deployed as stimuli and evaluated and systemised in terms of their signalling effect.

One of the most often used picture stimulus sets is the International Affective Picture System IAPS (Lang, Bradley, & Cuthbert, 2005). This set comprises hundreds of color photographs, which depict scenes of people, insects, snakes, spiders, attacks, diseases, mutilations, male and female nudes, erotic couples and many others. Beside pictures, sounds are also used to evoke emotions; for example the International Affective Digitized Sound system IADS (Bradley & Lang, 1999), which provides a set of acoustic emotional stimuli for

experimental investigations of emotion, including 167 sounds to induce emotions like fear, happiness, anger, sadness , and disgust.

Each stimulus in the IAPS and in the IADS is rated by a large group of people (both men and women) for the feelings of pleasure (valence) and excitement (arousal) that the stimulus evokes during perceiving. Affective ratings for valence and arousal differ on a 9-point rating scale. The valence scale ranges from 1 (very unpleasant), 5 (neutral) to 9 (very pleasant), while on the arousal scale 1 depicts the lowest (very calm), 5 the middle (neutral) and 9 the highest arousal level (very exciting).

Concerning the IAPS pictures it is noticeable that valence and arousal cannot be completely separated from each other. Pictures of a pronounced pleasant or unpleasant nature tend to lead to higher arousal ratings. When the pictures come under the head of "neutral", the arousal level is generally listed as lower. Moreover, it can be revealed that more pleasant pictures may be coupled with either a high or a low arousal level, whereas unpleasant pictures show a distinct concentration in the area of high arousal levels. This seems to indicate a correlation between valence/unpleasant and arousal/high. The more unpleasant a picture is perceived, the higher its arousal level is going to be. What applies to neutral pictures is that their arousal, if compared to the arousal of emotional valenced pictures, fails to reach equally high levels (see Figure 1).

Similar observations can be made when looking at the distribution of the arousal levels of the IADS sounds. There is also a tendency that unpleasant sounds have relatively high arousal levels, while the arousal levels of sounds in the realm of valence/neutral remain below the high levels of the sounds that are classed as pleasant or unpleasant (Bradley & Lang, 1999).

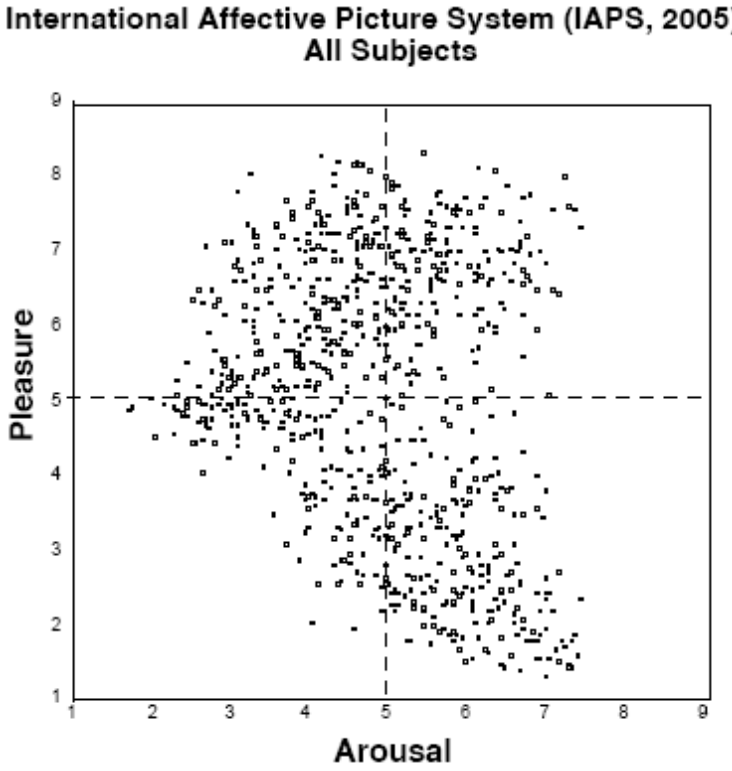

Figure 1. Normative ratings to IAPS pictures on valence and arousal dimensions (Lang et al., 2005).

It is a common, albeit rarely reflected experience in our day and media age that intense emotions may not only be triggered by pictures or sounds, but equally by music. When a film sequence moves us to tears, or frightens us, this may quite often be due to the underlying music rather than due to the pictures themselves. Music is emotionally effective (Koelsch, 2010). It brings about changes in the autonomous nervous system which are linked to different emotional states (Krumhansl, 1997). In the cortex pleasant and unpleasant sounds lead to different brain activations (Blood, Zatorre, Bermudez, & Evans, 1999). Emotional access to music seems to be universal by nature. In music, happiness, sadness and fear are recognized as three basic emotions across culture bounds (Fritz et al., 2009). As a result, some studies do indeed set out to enhance the effect of emotional stimuli by means of a combined presentation of pictures and music – mainly by applying classical musical excerpts (Baumgartner, Lutz, Schmidt, & Jäncke, 2006; Baumgartner, Willi, & Jäncke, 2007).

Memory

By definition, all acquisition of new information or knowledge is what we call "learning", whereas the retention of learned information is "memory". All information to be remembered follows the same pattern: encoding, storage and retrieval. Encoding equals the conversion of stimuli into a form that can be stored in memory. Storage refers to longer lasting retention of the encoded information. Retrieval includes the processing of stored information and its recall.

According to Atkinson & Shiffrin (1971) there are three distinct stages of memory: sensory memory which stores sensory impression for only one moment; short-term memory for information being held temporary; and long-term memory responsible for the permanent storage of information. The processes, whereby fragile memories are transformed into durable long-term memories with the passage of time, are referred to as memory consolidation (Shadmehr & Brashers-Krug, 1997). The long-term memory consists of two types in itself, namely explicit/declarative memory for facts and events; and implicit/procedural memory for motor skills and habits. It has been generally acknowledged that explicit memory can consciously be recollected, whereas implicit memory cannot (Schacter, 1987).

Motor Skill Memory

Proctor and Dutta (1995) define “skill” as follows: “Skill is a goal-directed, well-organized behaviour that is acquired through practice and performed with economy of effort”. Motor skill is gained through motor learning. Schmidt (1998) defines motor skill learning as a set of processes associated with practice or experience leading to relatively permanent changes in the capability of the movement. Changes usually occur during the practicing of common activities like riding a bicycle or playing the piano. We make progress and improve. We also consolidate our performance. This process enables us to apply the correct amount of force at the correct time and in the right direction (Wulf, 2007).

Motor learning processes can be divided into three temporal stages (Fitts & Posner, 1967): the cognitive stage, associative stage, and autonomous stage. The first stage is signified by a focused learner and is a conscious attempt to identify and learn (re-produce) the skill. The associative stage is focused on practicing the skill; the learner concentrates on picking and tuning the most efficient motion pattern to perfect the skill. In the autonomous stage skill becomes more and more automatic, until practicing needs little or no conscious involvement and is- at an expert level- nearly free of errors.

Motor learning evolves from an initial short-lasting stage into a subsequent functionally different stage (Brashers-Krug, Shadmehr, & Bizzi, 1996). In other words, the acquisition of a new motor skill follows two distinct stages with continued practice; an early, fast learning stage in which performance improves rapidly within a single training session (Karni et al., 1998) and a later stage, which involves processes known as consolidation (Walker, Brakefield, Hobson, & Stickgold, 2003). Motor memory consolidation can describe two different processes: motor memory may be enhanced, demonstrated by an improvement in performance between practice sessions, or it may be stabilized, by becoming less susceptible to interference (Robertson, Pascual-Leone, & Miall, 2004).

Explicit Memory and Emotion

Everyday life shows plenty of evidence that facts and events surrounding powerful emotions are better remembered than those devoid of emotional diversity. Flashbulb memories emphasise this effect as individuals record a lively, almost eidetic memory of a shocking and emotionally disturbing occurrence (Brown & Kulik, 1977; Heuer & Reisberg, 1990; Rubin & Kozin, 1984; Hirst et al., 2009).

Events that induce arousal notably lead to distinctive memory enhancement (Anderson, Wais, & Gabrieli, 2006; Bradley, Greenwald, Petry, & Lang, 1992; Buchanan,

Etzel, Adolphs, & Tranel, 2006; Cahill, Prins, Weber, & McGaugh, 1994; Cahill & McGaugh, 1995; Kensinger & Corkin, 2003; Talmi & Moscovitch, 2004).

While a vast number of studies concentrate on the arousal aspect, more and more research is being conducted into emotional valence and its impact on explicit memory. Kensinger and Corkin (2003) have proven that emotional words are recalled in more detail than neutral ones. The effect is at its peak when words carry arousal, but it is also to be observed when words have only valence. Ochsner (2000) has shown that memory can be enhanced even if positive or negative stimuli do not elicit arousal. Contributions of familiarity and recollection to the experience of recognising positive and negative stimuli varied though, since negative stimuli tended to be remembered more frequently than positive stimuli, whereas positive stimuli tended to be known more often than negative ones.

Recent studies have shown that memory for visual details can be manipulated by emotional valence. Subjects excel at discerning same from similar images when these images elicit negative rather than positive emotion (Kensinger, Garoff-Eaton, & Schacter, 2006, 2007; Kensinger & Schacter, 2008a).

Many times people remember the particulars of negative events while a positive event is merely remembered as having taken place, lacking detail (Kensinger, 2009). Surveys of autobiographical memories, however, indicate an advantage for positive events (D'Argembeau, Comblain, & van der Linden, 2005; White, 2002). Individuals striving for positive goals show enhanced memory in terms of positive events as opposed to negative ones (Mather & Carstensen, 2005).

Recently, Greene and colleagues (Greene, Bahri, & Soto, 2010) have demonstrated neither valence nor arousal alone but their interaction is important in modulation of explicit memory. After emotional induction, subjects completed a recognition test. The results showed memory enhancements both in positive mood-high arousal and in negative mood-low arousal conditions.

Finally we should notice that distinct brain systems seem to underlie the processing of valence and arousal. It has been suggested that effects of emotional arousal on memory rely on a neural network which includes the amygdala and the hippocampus (Cahill & McGaugh, 1998; Kensinger, 2004; Kensinger & Corkin, 2004) whereas effects of emotional valence are mediated by prefrontal and hippocampal structures (Anderson et al., 2003; Kensinger & Corkin, 2004; Kuchinke et al., 2006; Small et al., 2003).

Motor Memory and Emotion

It is explicit memory and its conscious recall of encoded data (Squire & Zola, 1996), which has been in the centre of interest for almost all previous studies investigating emotion regulation and memory. Motor skills however are independent from conscious recall, they are demonstrated through behavioural changes, but may also be influenced by emotion regulation (LaBar & Cabeza, 2006).

Much of our current knowledge about interactions between the emotion system and motor system comes from animal research, such as Pavlovian fear conditioning and inhibitory aversive training (McGaugh, 2004). It is a robust and acknowledged result as well in animals as in humans, that the startle reflex can be modulated by emotion (Andreatta, Mühlberger, Yarali, Gerber, & Pauli, 2010; Hillman, Hsiao-Wecksler, & Rosengren, 2005; Lang et al., 1990; Koch, 1999). This can be shown for many emotionally arousing stimuli (Bradley & Lang, 2000b; Vrana & Lang, 1990). A particular observation in this context is the enhancement of the magnitude of the reflex by negative emotion, whereas the experience of positive emotion can lead to its suppression.

A number of studies have demonstrated that passive viewing of pictures which induce emotions results in postural adjustments. For example, exposure to positive emotional stimuli accelerates approach movements, whereas exposure to negative cues elicits rapid avoidance movements (Chen & Bargh, 1999; Coombes, Cauraugh, & Janelle, 2007; Rotteveel & Phaf,

2004). Furthermore, participants show a freezing-like reaction when confronted with unpleasant stimuli unlike when exposed to pleasant or neutral stimuli (Azevedo et al., 2005; Facchinetti, Imbiriba, Azevedo, Vargas, & Volchan, 2006). Along with other many species, alerted human individuals react to danger motionlessly watching the source of threat and ready to fight or flight.

It has been recognized for many years that psychological factors play an important role in sport skills (Terry, 2004). Emotions affect performance in many different ways (Lazarus, 2000). In this way, the relationship between anxiety (emotional arousal) and athletic performance is widely studied. We know three distinguished arousal theories in sports: drive theory, optimal arousal theory (the inverted-U hypothesis), and reversal theory.

Hull (1943) set down the ground rules for drive theory which implies that there is a linear correlation between arousal and athletic accomplishment, especially when it comes to well-rehearsed skills. An athlete's performance increases with emotion and excitement. The more choreographed a skill is, the higher the probability of arousal advancing athletic performance. The optimum arousal theory originated with Yerkes and Dodson (1908). It presupposes the existence of a curvilinear relationship between arousal and athletic prowess. Performance increases with rising levels of arousal, albeit only to a point which generally sets in when the ideal arousal level is reached. As soon as the optimal arousal level is passed, performance declines. It is worthy of note that complex and simple skills may necessitate various optimal levels. Taking a closer look at reversal theory (Apter, 1989) we find that it is based upon the individual's interpretation of felt arousal which determines the way arousal affects performance. Depending on the situation, high arousal can be experienced as excitement or as anxiety.

Fundamental theories, findings and examples illustrate that emotions may affect motor behaviour and motor memory processes. The exact connections, modes of actions and underlying neuronal components, however, frequently require further and advanced research.

Experiment 1 – The influence of emotion on encoding of a motor skill memory

Introduction

Memory is about time-bound cerebral storage of information. Short-term memory refers to a limited period of data retention (Brown, 1964). Thus, it is considered to be an encoding process of information. Prior to the transfer of information to the permanent storage (long-term memory), it is encoded in the temporary storage (short-term memory).

Formation of explicit memory can be modulated by emotions (McGaugh, 2004; Phelps, 2004; Kensinger & Schacter, 2008b). According to various models of emotions we can observe two widely autonomous dimensions, valence and arousal (Lang, Bradley, & Cuthbert, 1997). While the valence dimension varies from negative to positive, the arousal dimension extends from deactivated to highly aroused states (Russell & Barrett, 1999). Successful recall of neutral material is differentially modulated by emotional context (Erk et al., 2003). Active recovery from explicit memory is enhanced for information encoded in positive emotional context as compared with neutral or negative context (Asby, Isen, Turken; 1999; Erk et al., 2003). Labar and Phelps (1998) have shown that arousal may have differential effects on short-term versus long-term explicit memory.

Motor memory is a set of processes associated with practice leading to relatively permanent changes in the capability of the movement (Schmidt, 1998). Classen and his colleagues (Classen, Liepert, Wise, Hallett, & Cohen, 1998) have shown evidence for short term memory for movement; training rapidly and transiently establishes a change in the cortical network, which encodes kinematic details of the practiced movement. Hajcak et al. (2007) provided evidence that motor cortex excitability is sensitive to emotional processing;

in their study viewing arousing stimuli, regardless of valence, modulated motor cortex excitability. An increase of brain activity in motor areas of the brain during emotional processing has been reported by some neuroimaging studies (Bremner et al., 1999; Rauch et al., 1996). To the present day, knowledge is lacking about effects of emotion on short-term memory of a motor skill. To address this issue, we used a motor task, in which subjects had to learn to control their muscle force utilizing their right thumb. While performing the motor task, the subjects heard emotional sounds in four different experimental conditions that varied in valence and arousal dimensions.

Methods

Participants

Sixty eight subjects (36 male, 32 female) participated in this study. The mean age of the subjects was 25.09 years (S.D. = 5, range: 21–40 years). All subjects were students recruited from the University of Würzburg, Germany. All subjects gave written consent for participation in the experiment. All subjects in the experiment received €8 for their participation.

Affective stimuli

The emotional sounds were selected from the International affective digitized sounds (IADS; Bradley & Lang, 1999) to engage a broad range of emotional responses, varying systemically in affective valence and arousal. This stimulus set was subdivided into four subsets of emotional sounds (each containing 6 emotional sounds) for valence and likely for arousal according to the mean ratings of a standardization sample of subjects provided by Bradley and Lang (1999). The four subsets of emotional sounds were as follows: 1. Valence negative / Arousal low (V-/A-), 2.Valence negative / Arousal high (V-/A+), 3. Valence positive / Arousal low (V+/A-), and 4.Valence positive / Arousal high (V+/A+) [1]. The sounds were selected on the basis of their mean ratings of valence (positive > negative) and arousal (high > low). Normative ratings of valence for pictures in these categories differed (V-/A-: 4.17, V-/A+: 3.98, V+/A-:7.1, and V+/A+: 7.12), as did normative ratings of arousal (V-/A-: 4.63, V-/A+: 6.37, V+/A-: 4.1, and V+/A+: 6.35) (Bradley & Lang, 1999).

[1] The numbers of IADS sounds used were as follows. (V-/A-): 370, 151, 206, 816, 810, 721.V-/A+: 401, 226, 111, 820, 815, 415. V+/A-: 358, 322, 702, 708, 280, 252. V+/A+: 292, 423, 310, 133, 710, 711.

Motor task

Subjects were asked to perform brisk isometric abductions with their right thumb (Stefan et al., 2006).The subject's force was recorded by a force transducer (Grass CP122A, Grass Instruments CO, West Warwick, RI) and the force signal was fed back to the subjects on a computer screen. The subject's individual force was established, and a target force window was defined as a range between 25 and 30% of the individual maximum force displayed as two horizontal lines on the computer screen (see Figure 2). As the display was scaled to the subject's individual maximum force in each experiment, the target window had the same geometrical size for all subjects. Each subject had to perform a total of 500 metronome-paced (0.5 Hz) isometric thumb abductions in a series of 5 training blocks that were separated by 30 s and consisted of 100 abductions each. A colour change (green) of the screen signalled the subjects each start of the required response (the abduction response).

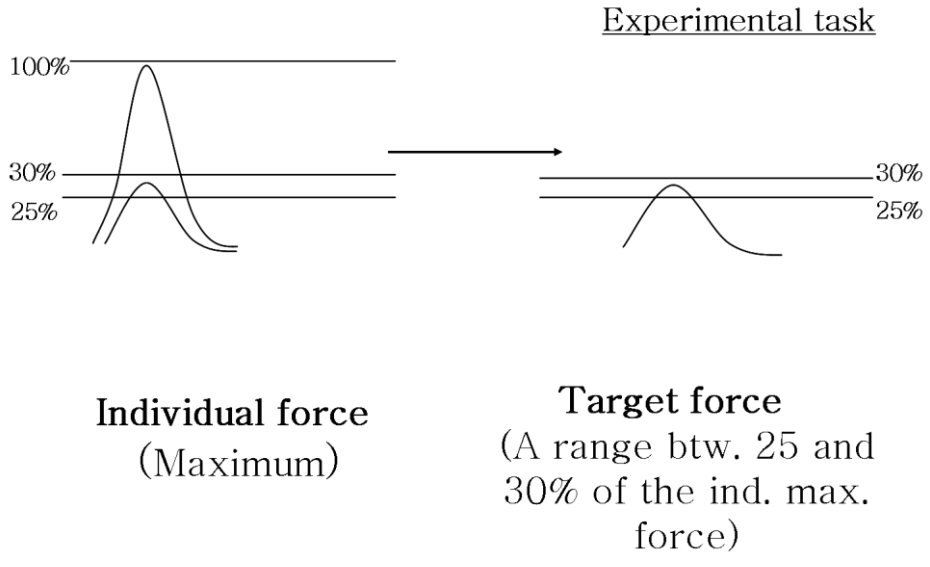

Figure 2. Subjects were instructed to perform abductions placing the executed force within the force window between the limits of 25 and 30% of maximum force.

Experimental Design

The experimental task (consisting of 5 blocks) lasted 20 min 40 s. Each block lasted 200 s. Within each block the same 6 sounds were played (each sound lasting 6 s) randomly. Between the sounds, at the beginning and at the end of each block there was a short pause lasting 1.31 s. In addition, between each block there was a pause lasting 1 min. While performing the motor task, the subjects heard emotional sounds in the four different experimental conditions. Sixty eight subjects were randomly and equally distributed between four experimental groups of 17 subjects each. Before the motor task subjects were simply instructed to respond as quickly and correctly as possible and to listen to the acoustic stimuli. At the end of the task the quality and intensity of emotional feelings were assessed by means of visual analogue scales (VAS, from 1 to 9): subjects were asked to rate their emotional feelings along the valence dimension (how pleasant or unpleasant they felt) and the arousal dimension (how intense the emotion was).

Data Analysis

The number of successful attempts was recorded for each training block. The primary outcome measure of motor learning was the difference between the mean number of hits achieved in the last training block, and the mean number of hits achieved in the first training block. For statistical analysis of the behavioural data, SPSS Statistics 17 for Windows (SPSS Inc., Chicago, IL) was used. Subjects' ratings of their feelings along the valence and the arousal scales were analysed by means of separate analyses of variance (ANOVA) with Group (V-/A-, V-/A+, V+/A-,V+/A+) as between-subject factor. Results are indicated as mean (± standard errors).An ANOVA for repeated measures was used to analyse performance (hits) at first and last blocks, with "block" (first and last block) as within-subjects factor. All results for performance improvements are indicated as mean ± SEM (Standard error). Effects of emotional interference on the primary outcome were analysed by means of ANOVA.

Between subjects factors were “valence” (negative and positive) and “arousal” (high and low).

Results

Behavioural ratings of emotional stimuli

Valence and arousal ratings. The mean valence ratings of positive and negative stimuli differed significantly from one another [$F(3,64) = 10.720$, $p<0.001$]. Post hoc comparisons confirmed that the valence ratings of V+/A- stimuli (6.2±0.1) were significantly higher than both V-/A- stimuli (4.3±0.1) and V-/A+ stimuli (3.7±0.1) (for both comparisons, $p<0.01$). The valence ratings of V+/A+ stimuli (5.9±0.1) were significantly higher than V-/A+ stimuli ($p<0.01$), and higher than V-/A- stimuli ($p< 0.05$), (see Table 1).

The mean arousal ratings of high and low groups differed significantly from one another [$F(3, 64) = 3.784$, $p<0.05$)]. Post hoc comparisons showed that V+/A+ stimuli were rated as more arousing than V-/A- stimuli ($p<0.05$), but V+/A+ stimuli were not significantly higher than V+/A- ($p=0.875$). The arousal ratings of V-/A+ stimuli were significantly higher than V-/A- stimuli ($p<0.05$), but V-/A+ stimuli did not differ significantly from V+/A- ($p=0.740$), (see Table 1).

Table 1. Mean Ratings for valence (V) and arousal (A) of emotional stimuli in the four groups after the experimental task

Emotional Stimuli	Valence	Arousal
V - / A -	4.3	3.7
V - / A +	3.7	5.6
V + / A -	6.2	4.6
V + / A +	5.9	5.6

Performance Improvements

There was no significant difference in performance between the experimental groups at block1 [F (3,64) = 2.608, $p<0.05$]. This suggests that all groups had equal performance at the beginning. The subjects' performances improved significantly between block1 and block 5 [F (1,64) = 22.023, $p<0.001$], (see Figure 3). While fifty-two subjects' performances improved between first and last block, the performances of sixteen subjects did not improve.

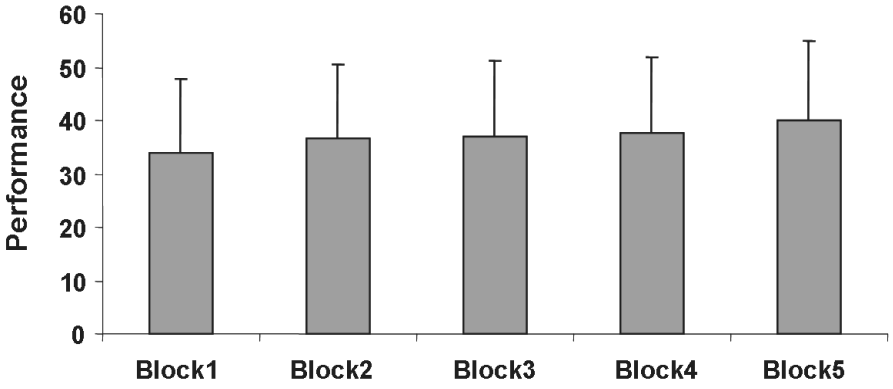

Figure 3. The mean Performance Improvements across blocks. Error bars show standard deviation.

However, the improvement in performance was not significantly influenced by valence [F (1,64) = 1.071, p=0.305], arousal [F (1,64) =0.028, p=.867], or their interaction [F (1,64) = 0.487, p=.0.488], (see Figure 4).

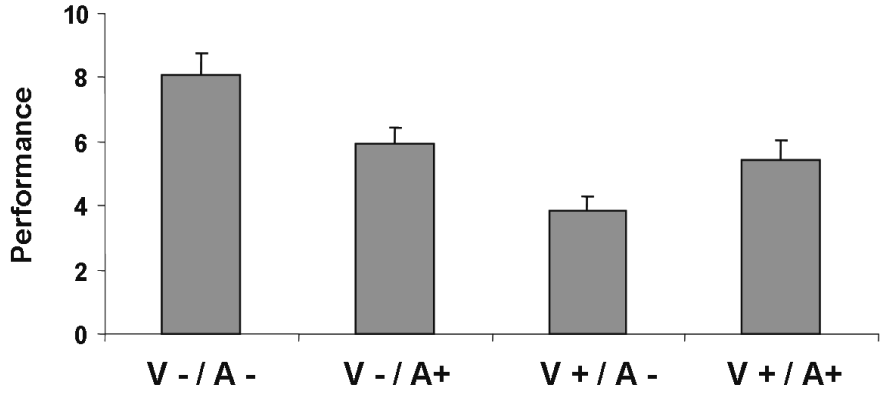

Figure 4. The mean Performance Improvements between block1 and block5 across groups. Error bars show standard error

Discussion

The aim of this study was to investigate the influence of emotion on the short term memory of a motor skill. The analysis of the complete data did show best performances for motor learning in the V-/A- condition, but the results between the conditions were not significant.

It has long been known that experiences that elicit arousal are more likely to be remembered than experiences that do not evoke an emotional response. There is extensive evidence for arousal–mediated enhancement of memory, with positive and negative events more likely to be remembered than non-arousing ones (Anderson et al., 2006; Buchanan et al., 2006; Kensinger & Corkin, 2003; Talmi & Moscovitch, 2004). When it comes to remembering the details of the information, however, emotional events with negative valence are recollected more accurately than positive ones (Kensinger, 2009). For example, sensory features of an object are better retained when the images elicit negative emotion than when they elicit positive emotion (Kensinger et al., 2006, 2007; Kensinger & Schacter, 2008a).

In our study the best performances are observed in low arousing negative valence condition. Similarly, Greene et al. (2010) reported that the negative mood-low arousal state enhanced recognition memory for following abstract shapes. They suggested that

“melancholic” states may be associated with the formation of more finely detailed memory representations. The observed best performance in the V-/A- condition in our study could also be explained by the optimum arousal theory (Yerkes & Dodson, 1908). Performance grows with growing arousal, but it performs in such way only up to a level that is usually reached with the ideal level of arousal. Performance declines once the threshold (optimum arousal level) is crossed.

The absence of any significant difference between groups may be explained by several reasons: Firstly, the induction of emotion probably did not work well enough for one group; the arousal ratings of V+/A- did not differ significantly from V+/A+ and V-/A+. As emotions can be interpreted differently dependent on personality type, a screening test in advance would be useful to detect for example low-trait or high-trait anxious subjects. Bradley and colleagues (Bradley, Mogg, Falla, & Hamilton, 1998) found that highly anxious subjects selected on trait anxiety compared with the low-anxious subjects, showed an attentional bias toward threatening emotional stimuli. Another explanation for insufficient emotional induction might be the emotional stimulus itself. Although the mean standardized arousal ratings of the experimental groups differed significantly from another, the sounds of V-/A- and V+/A- groups were not very low in arousal. In the IADS stimulus set (Bradley & Lang, 1999) there are no sounds which are very low on the arousal scale and concomitantly very low or very high on the valence scale. It is therefore questionable if the IADS stimulus set is a good choice for investigation of such valence and arousal interactions like V-/A- and V+/A- Future experiments on emotional modulation should consider this issue.

Secondly, the task difficulty between conditions may have caused irregularities in the performance of our subjects. Some subjects were not able to improve their performances between first and last block. Although the emotional interference might have caused performance deteriorations, it might also be that the motor task was fatiguing for some subjects; therefore their performances could not show any performance improvements.

In sum, the current experiment was a first step in considering the effects of emotion on motor learning. Although some methodological problems cannot be ruled out, the best performances in the V-/A- condition suggest that for encoding of motor skill memory negative valence and low arousal may be more effective. However, future studies are needed to validate this assumption.

Experiment 2 - Emotion and the Consolidation of Sequence Learning in humans

Introduction

Procedural memory includes memory for motor skills, e.g. remembering how to drive a car, to swim, or to use a keyboard. Hence, it is very important in daily human motor performance. It may occur without conscious knowledge of the rules which have to be learnt, as opposed to declarative memory which presupposes awareness of the learning process and contents (Willingham, Salidis, & Gabrieli, 2002). The neural underpinnings of these two memory systems seem to be separate. Previous studies have shown that declarative memory is subserved by the hippocampus, while the striatum, a part of the basal ganglia, supports procedural memory (Squire & Zola, 1996; Squire, 1992).

Consolidation of motor memory refers to a process whereby a newly acquired skill is transformed into a strong and stable engram rendering it robust toward interference. For consolidating this skill, some elapse of time is required (Brashers-Krug et al., 1996). However, in addition to being stabilized, skill performance can also be enhanced in the absence of practice (off-line learning) (Robertson et al., 2004; Walker, 2005). The progress of the consolidation can be monitored by testing whether and how much the memory is susceptible to disruption by a competing experience during a limited time window (Krakauer & Shadmehr, 2006). For example, a second skill learning task can perturb any form of consolidation of a newly acquired skill if processed immediately after the acquisition of the first skill (Brashers-Krug et al., 1996; Walker et al., 2003). This interference effect decreases with time elapsing between the two tasks; it is stronger for short, and weaker or absent for long time intervals. With the passage of time after the first skill learning task, the interference effect is first reduced and then lost at about 5-6 hours post-training (Brashers-Krug et al.,

1996; Walker & Stickgold, 2004; but see Baraduc, Lang, Rothwell, & Wolpert, 2004). Similar time-dependent consolidation can be revealed if the post-training intervention is not by performance of a second learning task, but by brain stimulation (Muellbacher et al., 2002; Baraduc et al., 2004; Reis et al., 2009).

A task frequently used to investigate motor learning is the serial reaction time task (SRTT) in which subjects have to learn new motor sequences (Nissen & Bullemer, 1987). Post-training performance of sequential learning can be influenced by many factors, such as the duration of the post-training interval (Walker et al., 2003), sleep (Fischer, Hallschmid, Elsner, & Born, 2002; Walker, Brakefield, Morgan, Hobson, & Stickgold, 2002), circadian rhythms (Cajochen et al., 2004; Keisler, Ashe, & Willingham, 2007), subjects' awareness of the sequential material (Robertson, Pascual-Leone, & Press, 2004), daytime naps (Nishida & Walker, 2007), learning a word list (Brown & Roberson, 2007), the amount of training (Karni et al., 1998), in agreement with the concept of consolidation.

It has been shown that consolidation of declarative memory can be modulated by emotions (Erk, Martin, & Walter, 2005), more precisely, by semantically unrelated stimuli (Nielson & Bryant, 2005). In addition, the time interval at which emotional interference occurs is important for the consolidation of declarative memory (Nielson & Powless, 2007). Little is known, however, about similar influential effects of emotional stimuli on the consolidation of human procedural learning. To address this issue, we employed a SRTT. We tested the effect on post-training consolidation by emotional stimuli of different valence presented at two different times after training.

Methods

Participants

One hundred and thirty-eight healthy subjects (61 male, 77 female; aged 20-34 years) participated in this study. The study was approved by the ethics committee of the Medical Faculty at the University of Würzburg. All subjects were students recruited from the University of Würzburg, Germany and gave written informed consent for participating in the experiment. All subjects in the experiment received €20 for their participation.

SRTT

All participants were asked to perform a modified version of the SRTT (Nissen & Bullemer, 1987). A filled circle cue (diameter 20 mm, viewed from 80 cm) was chosen to randomly appear in one of four possible horizontally spaced positions, numbered 1–4 on a monitor. These positions were assigned to one of the four buttons on a response pad, respectively (RB-730; Cedrus, San Pedro, CA). The participant rested his/her index and middle fingers of both hands on the buttons. When a target appeared, participants were instructed to respond by pressing the corresponding button on the pad. No information has been given about any sequential presentation of the cues. When the participant's response was incorrect, the stimulus was upheld until the participant selected the correct button. After the correct response was given, the cue on the screen vanished. The next cue was presented on the screen after a delay of 400 ms. The positions of the visual cues were determined by a repetitive 12-item sequence which was identical for all subjects (2-3-1-4-3-2-4-1-3-4-2-1).

All subjects performed two SRTT sessions on two different days. The first SRTT session (session-1) principally served to acquire the skill and to establish a baseline performance of the skill for each subject. This session consisted of a short training block with 15 repetitions of the sequence (180 trials), a longer training block with 25 repetitions (300 trials), and a test block with 15 repetitions (180 trials). The second SRTT session (session-2), performed after 72 h, served to establish the subject's performance of the skill for comparison

with the subject's baseline as determined in the first SRTT session. The second session consisted of a single test block with 15 repetitions (180 trials) of the sequence. For all blocks, 50 random trials preceded and followed the sequential trials (see Figure 5). Within the random trials there were no repeats (e.g., -1-1 or -2-2), nor were there any "salients" such as "1-2-3-4". Each set of random trials in the training and test blocks was unique. However, the random trials were identical across all groups (Brown & Robertson, 2007).

Emotional Stimuli

The emotional interference was induced by presenting subjects pictures taken from the International Affective Picture System (IAPS; Lang, Bradley, & Cuthbert, 2005). Among these, we chose 36 positive (pleasant), 36 negative (unpleasant) and 36 neutral scenes. Positive pictures included happy families, nature scenes and puppies; neutral pictures included neutral faces and household objects; negative pictures included scenes of attack and threat[2]. Normative ratings of valence for pictures in these categories differed (positive: 7.7, neutral: 5.1, negative: 2.7), as did normative ratings of arousal (positive: 4.8, neutral: 3.3; negative, 5.4; Lang et al., 2005). Each picture was presented on a 19-inch computer screen with a frame refresh rate of 60 Hz. The stimuli were presented using Superlab (version 4.0.5).

[2] The numbers of IAPS pictures used were the following: positive (1440, 1441, 1620, 1710, 1721, 1920, 1999, 2040, 2070, 2091, 2216, 2260, 2311, 2332, 2345, 2352.1, 2388, 2395, 2398, 2550, 4626, 5200, 5480, 5600, 5621, 5830, 5831, 5833, 7580, 8210, 8380, 8496), negative (1111, 1220, 1525, 2205, 2375.1, 2455, 2590, 2703, 6020, 6212, 6243, 6360, 6540, 6570, 6836, 9001, 9041, 9180, 9220, 9290, 9421, 9426, 9428, 9435, 9470, 9530, 9560, 9810, 9901, 9902, 9903, 9910, 9911, 9913, 9925, 9926), and neutral (2200, 2214, 2372, 2745.1, 5395, 5471, 5510, 5531, 5920, 6150, 7002, 7004, 7006, 7036, 7037, 7043, 7056, 7057, 7090, 7100, 7160, 7170, 7179, 7182, 7185, 7207, 7211, 7233, 7235, 7236, 7247, 7546).

In order to enhance the emotional impact, pictures were paired with music or sound evoking a matched emotion (Baumgartner et al., 2006). The Adagio for Strings by Samuel Barber was chosen to evoke sadness and the Symphony no.6 (3rd mvt) by Beethoven to evoke happiness (Krumhansl, 1997; Peretz, Gagnon, & Bouchard, 1998).

The sound of walking shoes, derived from the International Affective Digitized Sounds (Sound No: 722), was presented as neutral sound (IADS; Bradley & Lang, 1999).

Experimental Design

At the very beginning of the experiment, we ran a screening trial in order to assure that the different emotional stimuli elicited congruent emotional states in the subjects. During this screening, a total of 30 pictures, divided into three categories (10 neutral, 10 pleasant, 10 unpleasant) were presented for 6 seconds each. Pleasant pictures were combined with the happy music; unpleasant pictures with the sad music and neutral pictures with the neutral sound. The three emotional categories were presented with a blocked design and with random order across subjects. At the end of this stimuli presentation, subjects were asked to name each picture set, according to the three emotional categories (neutral, pleasant or unpleasant).

Within each emotional category, multiple pictures were given preference over displaying a single picture to ensure that subjects maintained attention to the task and that induction of emotion was independent of the specific contents of the emotional picture. Before starting the SRTT task, subjects were shown 36 neutral pictures combined with the neutral sound. This procedure served to induce the same level of neutral mood in all participants. During this neutralization phase, pictures were visible for 6 s with no inter-stimulus interval and presented twice randomly. Afterwards, subjects performed the SRTT task.

After completing the three blocks of the SRTT task, the intervention based on the emotional interference began. Subjects were shown a set of pictures while listening to the

matched musical background (pleasant, unpleasant or neutral). During this phase, 36 pictures were visible for 6 s with no inter-stimulus interval, and presented three times in a random order (see Figure 5).

The three types of emotional interference (negative, positive, neutral) were applied in one of two different time intervals: either immediately, or 6 hours after completion of the first SRTT session. Hence, subjects were randomly assigned to the six different conditions: Negative-0 hours (Neg-0), Negative-6 hours (Neg-6), Neutral-0 hours (Neu-0), Neutral-6 hours (Neu-6), Positive-0 hours (Pos-0), and Positive-6 hours (Pos-6).

The quality and intensity of emotional feelings were assessed at three different timings by means of visual analogue scales (VAS, from 1 to 9): at session-1 after the neutralization phase, after the emotional interference intervention and at session-2 after the neutralization phase. More specifically, subjects were asked to rate their emotional feelings along the valence dimension (how pleasant or unpleasant they felt) and the arousal dimension (how intense the emotion was). Furthermore, at session-2 after finishing the task, we investigated any eventual ability to recall the sequence, by asking general questions as: “Did you notice anything special about the task?” and “Do you have anything to report regarding the task?”. Subjects who noticed a sequence or repeating pattern, were asked to describe it in as much detail as possible, by telling how the sequence was or by reproducing the sequence with their fingers on the response button. The information gathered was documented by the experimenter for further analysis.

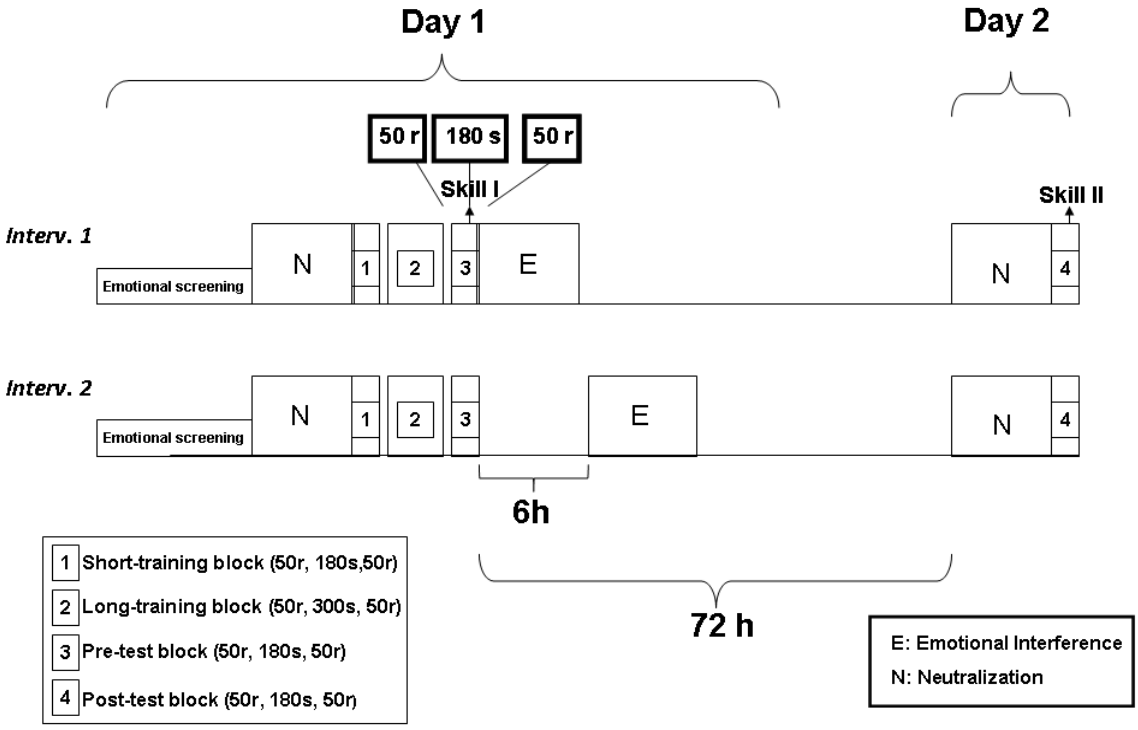

Figure 5. Subjects were initially trained on a serial reaction time task (skill testing I), the SRTT, then they were exposed to emotional stimuli consisting of a set of emotional pictures along with emotional musical stimuli. Emotional interference for each subject group was applied at one of two different time intervals (first group directly after the first SRTT session, second group 6 h later). After a 72 h interval, each group was retested (skill testing II) on the SRTT. Pre- and post-test blocks consisted of a single test block with 15 repetitions (180 trials) of the sequence. For both blocks, 50 random trials preceded and followed the sequential trials.

Data Handling

Performance was measured as speed (response time) and accuracy. Response time was defined as the interval between the onset of a visual cue on the screen and the selection of the corresponding button (correct response). In each block, response times longer than 2.7 standard deviations (i.e. the top one percentile) from a participant's mean and those exceeding 2000 ms were removed. Accuracy was defined as the number of errors in each experimental condition.

The primary outcome of the study was the intervention-related change in performing the SRTT. Training- or intervention-related changes in the SRTT performance can be twofold: improvement of *general performance* or improvement of a *specific skill*. General performance changes of speed and accuracy should emerge both in sequential and random trials, whereas specific skill changes should be confined to performance in the trained sequence and, therefore, be unveiled as a difference between sequential and random trials.

General performance. Improvement of response times even for random stimuli is demonstrated by previous experiments (Nissen & Bullemer, 1987). Therefore, as a measure of general performance we computed the mean response time (RT) and number of errors in the final 50 random trials of session-1 and session-2. We chose to average performance at the final 50 trials in order to rule out any effect due to the initial familiarisation with the task and the experimental setting. Hereafter, when we refer only to "random", we mean the average of 50 trials.

Specific skill. SRTT skill (speed and accuracy) was computed as follows: a baseline score at session-1 (Skill_d1) was calculated by subtracting mean performance at the final sequential trials from mean performance at the final random trials (Skill_d1: final random – final sequential) (Nissen & Bullemer, 1987; Willingham, Nissen,& Bullemer, 1989) (see Figure 5).

Two different scores were calculated to assess skill after the intervention on session-2. Skill_d2 was calculated by subtracting mean performance at the final sequential trials from mean performance at the final random trials (Skill_d2: final random – final sequential). In addition, on session-2, Skill_d2* was calculated by subtracting performance at the first 50 sequential trials from performance at the first 50 random trials (Skill_d2*: first random – first sequential). By computing performance in the first trails of session-2 (Skill_d2*), we aimed at investigating any effect of the emotional intervention before practising the SRTT task again.

Differences between these scores gave a measure of the changes in the SRTT skill specifically due to the intervention with the emotional interference (*skill change*: Skill_d2 – Skill_d1, and *skill change**: Skill_d2* – Skill_d1).

Sequence knowledge. We were also interested in gauging the subjects' awareness of a hidden sequence and in the question of how many subjects in the six groups could explicitly recall the sequence in terms of items correctly remembered in the right position.

Data Analysis

Outliers, defined as subjects having a Skill_d1 performance higher or lower than 2.7 standard deviations (i.e. the top or bottom 1 percentile) from the group mean, were removed in each group. Overall, 23 subjects were considered for analysis in the Neg-0 group (13 females) and 23 subjects were considered for analysis in the Neg-6 group (13 females). Twenty-two subjects were considered for analysis in the Neu-0 group (12 females) and 22 subjects were considered for analysis in the Neu-6 group (13 females). Twenty-three subjects were considered for analysis in the Pos-0 group (13 females) and 22 subjects were considered for analysis in the Pos-6 group (13 females).

Valence and arousal ratings. Subjects' ratings of their feelings along the valence and the arousal scales were analysed by means of separate one-way analyses of variance (ANOVA) with Group (Neg-0, Neg-6, Pos-0, Pos-6, Neu-0, Neu-6) as between-subject factor. Results are indicated as mean (± standard errors).

General performance. In order to determine any initial difference in performance between groups, we analysed (one-way ANOVA) response times and accuracy of the six groups before emotional interference (Skill_d1). Any change of RT in *general performance* was analysed by

means of separate ANOVAs on the random trials with EMOTION (negative, positive, neutral) and TIME OF INTERVENTION (0 hours, 6 hours) as between subjects factors. Paired t-tests were used to compare the RT to the random trials at session-1 vs. session-2.

Specific skill. Effects of emotional interference on *specific skill* (RT and error rates) were analysed by means of ANOVAs, one for the first skill performance score (*skill change*) and one for the second performance score (*skill change**). Between subjects factors were EMOTION and TIME OF INTERVENTION. Paired t-tests were used to compare skill at session-1 with skill at session-2 (Skill_d1 vs. Skill_d2; and Skill_d1 vs. Skill_d2*).

Sequence knowledge. We carried out two further analyses in order to investigate whether the subjects' explicit knowledge of a sequence in the SRTT could have influenced their performance. Spearman's correlation coefficient was used to correlate skill improvements (*skill change* and *skill change**) with the explicit recall of the correct sequence positions and explicit awareness of a hidden sequence participants. Finally, we used Pearson chi square analysis to examine the relation between sequence awareness and emotional interference.

Results

Behavioural Ratings of Emotional Stimuli

Neutralization. The valence and arousal ratings of emotional stimuli in the six groups did not differ significantly after neutralization on session-1 and session-2 ($F<1$, $p>0.05$ for both sessions), (see Table 2).

Valence and arousal ratings. The valence ratings given by the three groups (negative, neutral, and positive) after emotional interference were significantly different [F (2,132) = 83.665, $p<0.001$]. Post hoc comparisons confirmed that the valence ratings of positive stimuli (7.2±0.2) were significantly higher than both neutral (4.9±0.2) and negative stimuli (3.3±0.2), and valence ratings of neutral stimuli were significantly higher than negative stimuli (for all comparisons, Bonferroni corrected $p<0.001$). Mean arousal ratings for negative (6±0.3), neutral (4±0.3) and positive stimuli (4.3±0.3) were significantly different [F (2,132) = 14.138, $p<0.001$)]. Post hoc comparisons showed that both positive and neutral pictures were rated as less arousing than negative ones (for both comparisons, Bonferroni corrected $p<0.001$), (see Table 2). However, arousal ratings for neutral and positive stimuli were not significantly different (Bonferroni corrected $p>0.05$).

Table 2. Mean Ratings for valence (V) and arousal (A) of emotional stimuli in the six groups after neutralization on day 1, after emotional interference and after neutralization on day 2

	Pre-learning Neutralization(d1)		**Emotional Interference**		**Pre-test Neutralization (d2)**	
	V	**A**	**V**	**A**	**V**	**A**
Neg-0	5.3	3.6	3.4	5.7	5.1	3.9
Neg-6	5.3	3.5	3.2	6.3	5.2	4.0
Neu-0	5.1	4.1	4.9	4.1	5.3	4.4
Neu-6	5.2	3.9	5.0	4.0	5.2	4.3
Pos-0	5.3	4.0	7.1	4.6	5.1	3.8
Pos-6	5.3	4.1	7.4	3.9	5.2	4.2

General Performance

All experimental groups improved after completion of the SRTT training. At initial testing [ANOVA, F (5,129) =1.154, p=0.335] the experimental groups showed no significant difference in skill (Skill_d1), indicating that all groups started from similar skill levels before being exposed to the emotional stimuli. RTs to random trials during session-2 were shorter than session-1 [t(134) =8.165, p<0.001], but this reduction was not significantly influenced by EMOTION [F(2,129) =1.278, p=0.282], the TIME OF INTERVENTION [F(1,129)=0.045, p=0.832] or their interaction [F(2,129)=1.318, p=0.271], (see Figure 6).

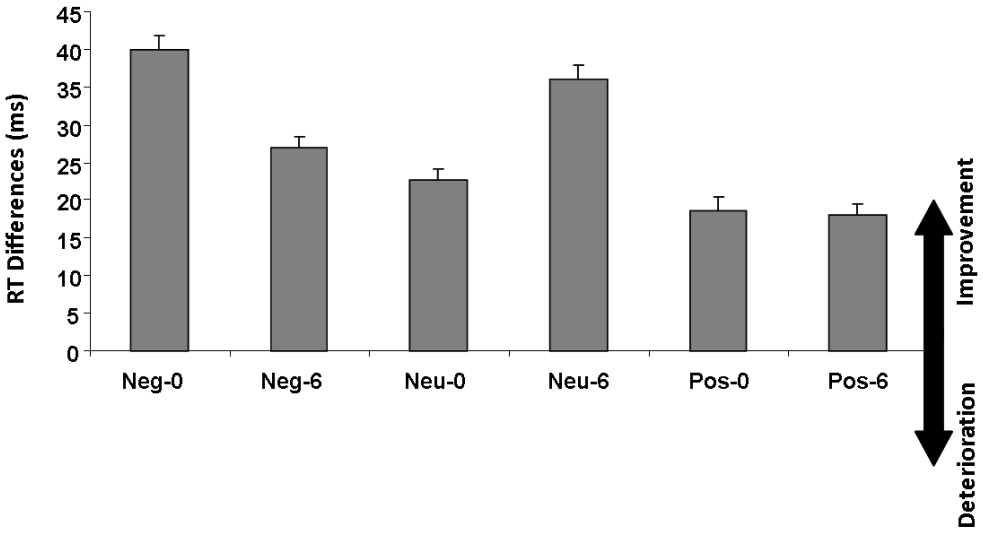

Figure 6. RT differences for random trials (session-2 minus session-1). Error bars show standard error.

The rate of errors committed in random trials was not significantly different at session-2 compared to session-1 [t(134)=0.625, p=0.533]. The differences were not distinctly influenced by either EMOTION [F(2,129)=0.729, p=0.485], or TIME OF INTERVENTION [F(1,129)=2.182, p=0.142], or their interaction [F(2,129)=0.043, p=0.958].

Specific skill

Skill change. Response time at retesting after 72h (Skill_d2) did not differ significantly from the response time before the interference (Skill_d1) [t(134)=.071, p=0.944]. In the analysis of *skill change* (Skill_d2 – Skill_d1) we found no significant effects of EMOTION [F(2,129) =0.092, p=0.921], of TIME OF INTERVENTION [F(1,129) =0.021, p=0.884] or of their interaction [F(2,129) =0.881, p=0.417], (see Figure 7a).

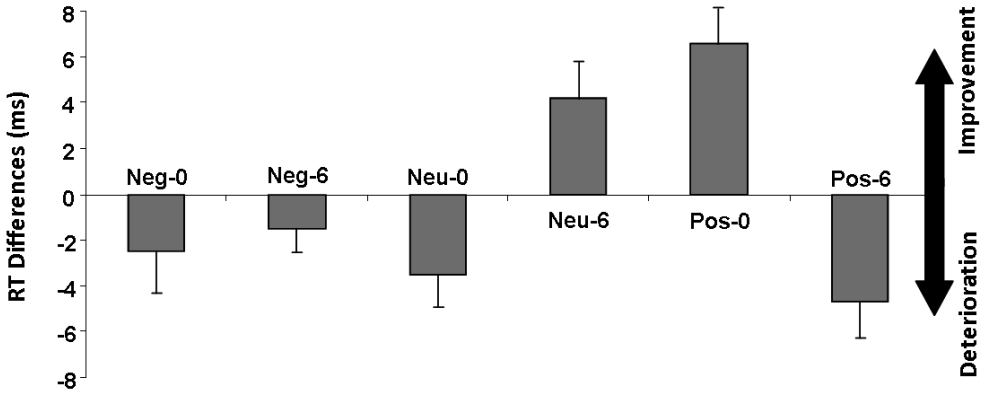

Figure 7a. RT differences for skill (Skill_d2 **–** Skill_d1) across groups. Error bars show standard error.

The rate of errors committed in skill was significantly reduced at session-2 (Skill_d2) compared to session-1 (Skill_d1) [t(134)=-2.799, p<0.01]. The differences were not distinctly influenced by either EMOTION [F(2,129)=0.298, p=0.743], or TIME OF INTERVENTION [F(1,129)=0.044, p=0.833], or their interaction [F(2,129)=0.049, p=0.952], (see Figure 7b).

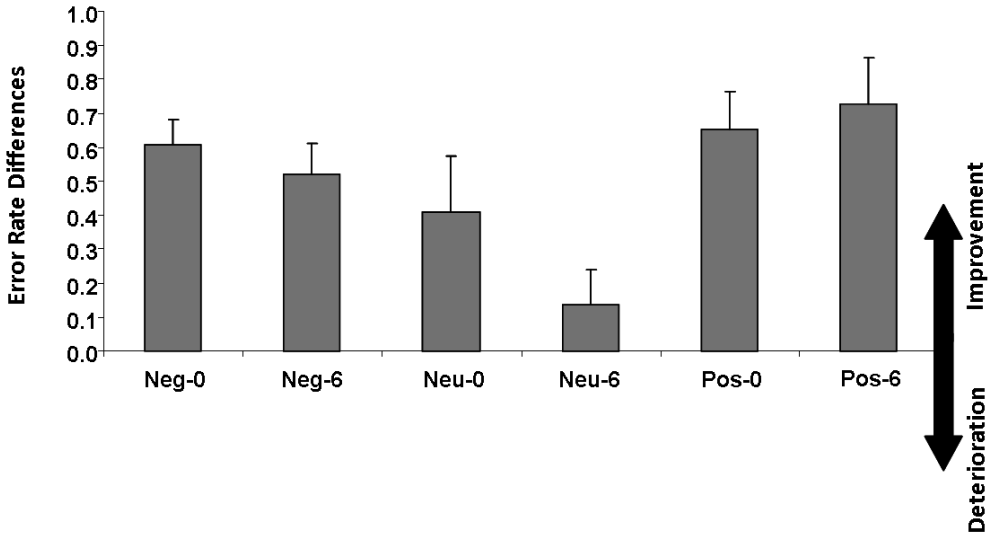

Figure 7b. Error rate differences in skill (Skill_d2 – Skill_d1) across groups. Error bars show standard error.

Skill change*. At retesting after 72 h, skill (Skill_d2*) had significantly deteriorated compared to skill before the interference (Skill_d1) [$t(134)=7.999$, $p<0.001$]. The analysis of the difference between these two skill indices (Skill_d2*– Skill_d1) revealed that *skill change** was not significantly affected by EMOTION [$F(2,129)=2.323$, $p=0.102$], by TIME OF INTERVENTION [$F(1,129)=0.056$, $p= 0.814$) or by their interaction ($F(2,129)=0.260$, $p= 0.771$), (see Figure 8a).

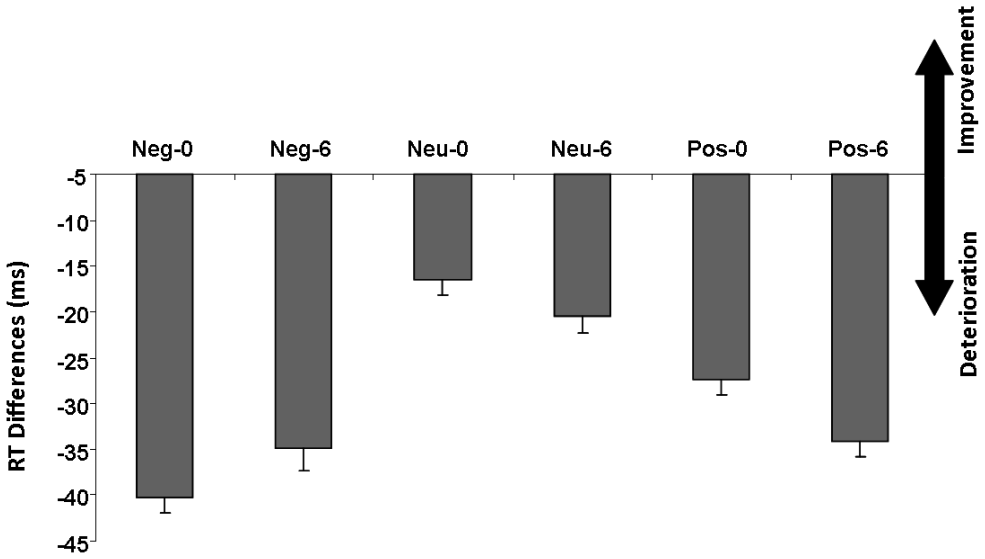

Figure 8a. RT differences for skill (Skill_ d2* – Skill_ d1) across groups. Error bars show standard error.

The rate of errors committed in skill was not significantly changed at session-2 (Skill_d2*) compared to session-1 (Skill_d1) [t(134) =1.212, p=0.228]. The differences were not distinctly influenced by either EMOTION [F(2,129) =0.397, p=0.673], or TIME OF INTERVENTION [F(1,129)=2.320, p=0.130], or their interaction [F(2,129)=2.214, p=0.113], (see Figure 8b).

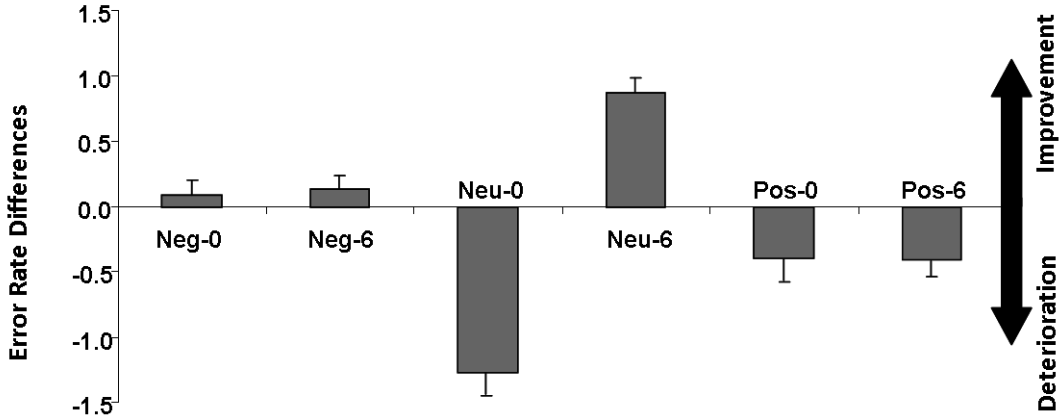

Figure 8b. Error rate differences in skill (Skill_ d2* – Skill_d1) across groups. Error bars show standard error.

Sequence knowledge

There was no significant correlation between participants' recall of the sequence and the induced improvements (*skill change*, r=0.157, p=0.070), (skill change*, r=0.045, p=0.603). The correlation between the induced improvements and sequence awareness was also not significant (skill change, r= 0.136, p=0.115), (skill change*, r=0.043, p=0.622).

The Pearson Chi-Square test showed that the relation between EMOTION and sequence awareness was significant [(X^2 (2, N=135) = 8.631, p=0.013]. In the negative-valence group more subjects noticed a sequence compared to the positive- and the neutral-valence groups (see Table 3).

Table 3. Sequence x Emotion Crosstabulation

Sequence	EMOTION			Total
	Neg	Neu	Pos	
Yes	40	27	29	96
No	6	17	16	39
Total	46	44	45	135

When each time interval was examined separately, a significant difference in the negative-valence group was present only for the 0-hour interval, [X^2 (2, N=68) = 9.235, p=0.010] (see Table 4), but not for the 6-hour interval [X^2 (2, N=67) = 2.063, p=0.357] (see Table 5).

Table 4. Sequence x Emotion Crosstabulation in 0-hour interval

Sequence	EMOTION			Total
	Neg-0	Neu-0	Pos-0	
Yes	21	11	15	47
No	2	11	8	21
Total	23	22	23	68

Table 5. Sequence x Emotion Crosstabulation in 6-hour interval

Sequence	EMOTION			Total
	Neg-6	Neu-6	Pos-6	
Yes	19	16	14	49
No	4	6	8	18
Total	23	22	22	67

Discussion

The present study aimed to investigate the effects of emotional interference on the consolidation of a serial reaction time task (SRTT). After neutralization, and after emotional intervention, subjects confirmed the *a priori* classification of emotional valence and arousal, suggesting that the stimuli were correctly interpreted and were likely to evoke different emotional states (Halberstadt & Niedenthal, 1997). We found no significant influence of emotional stimuli on SRTT skill after an interval of 72 hours, neither on speed nor on accuracy. However, the emotional interference directly after learning had a differential effect upon the explicit awareness of the implicitly acquired sequence. Specifically, the induction of a negative emotion enhanced the subjects' awareness of a hidden sequence in the task.

The reduction of RT in general performance during session-2 compared to session-1 hints at significant gains across a 72-hour break, whereas accuracy in performance was maintained. This indicates that the participants showed off-line enhancements in performance speed. However, improvements were not modulated by emotional interference. As we were predominantly interested in specific skill changes, we focused on the question of whether RT after the interference (Skill_d2) would differ significantly from RT before the interference. Speed in skill was maintained across a 72-hour break after the interference, whereas accuracy in skill was significantly improved off-line between sessions. However, emotional interference did neither affect subject performance in speed across groups (as shown in Figure 7a) nor skill improvements in accuracy (as shown in Figure 7b). After the interference, skill (Skill-d2*) had significantly deteriorated in terms of speed, whereas accuracy in skill was maintained. Yet, interference did neither affect subject performance in speed (as shown in Figure 8a) nor in accuracy (as shown in Figure 8b). In summary, following a 72-hour break, skill-related speed was lower at the beginning of the second session, compared to the end of the first session. But at the end of session-2 it improved again, while its level was not

significantly different than at the end of session-1. Skill-related accuracy was maintained at the beginning of session-2, and even significantly enhanced by the end of it, following a 72-hour break. These changes were not affected by the interference of emotion, time or their interaction.

Previous studies investigating sequence learning or sequence tapping have shown contrasting results regarding time-dependent consolidation effects. Using a finger tapping task, in which subjects were required to press a recurring five-element sequence, Walker and colleagues (2003) showed off-line improvements both in accuracy and speed after a break of 24 and 72 hours. Off-line skill improvements have been observed after a 12-hour break, irrespective of sleep, when subjects acquired a SRTT skill unintentionally. Sleep-dependent improvements, however, have been observed when participants intentionally acquired the SRTT skill (Robertson et al., 2004), whereas in another SRTT study sleep did not enhance implicit motor sequence learning (Fischer, Drosopoulos, Tsen, & Born, 2006). In yet another study, subject performance showed no evidence for time dependent consolidation (Goedert & Willingham, 2002), while Willingham and Dumas (1997) observed retention of general skill but not sequence-specific improvements after a one-year delay. Song, Howard, and Howard (2007) used a probabilistic sequence learning paradigm, where certain sequences occur at a higher frequency than others, to investigate off-line consolidation. Their results showed that sleep did not enhance general skill or sequence-specific learning, whereas the simple passage of time during the day enhanced general skill but not sequence-specific learning. In contrast, in another study (Nemeth et al., 2010) general skill learning improved off-line over the day as well as over a night of sleep, while sequence-specific off-line improvements occurred in neither condition. Clearly, no uniform pattern of consolidation effects on either general or specific skill emerges from these studies, suggesting that differences between SRTT paradigms, the duration of consolidation intervals and the behaviour during the post-training interval may be important determinants whose precise roles are not yet understood. In our

study off-line improvements over 72 hours were observed in general performance, whereas speed of sequence-specific performance was only preserved. These results are consistent with studies of sequence consolidation, which demonstrated improvements in general performance, but not in sequence-specific skill (Willingham & Dumas, 1997; Fischer et al., 2006; Nemeth et al., 2010).

As subjects acquire skill producing a sequence while performing the SRTT, they can also acquire an ability to verbally describe some or all of the sequence (Nissen & Bullemer, 1987; Willingham et al., 1989; Robertson, 2007). This phenomenon of explicit acquisition for the sequence order verifies that the SRTT includes an essential declarative aspect. In the present study, the experimental groups differed in their performance in terms of noticing a hidden sequence, as in the negative-valence (0 h) group more subjects were able to notice a hidden sequence than in the other groups. Thus, these results suggest that explicit awareness was modified by the emotional interference. In a recent study (Brown & Robertson, 2007) disrupting the declarative component of the SRTT allowed off-line improvements in skill-specific changes, whereas when declarative knowledge for the motor skill was not disrupted, there was no enhancement of motor skill. Using a motor adaptation task, Keisler & Shadmehr (2010) observed similar interaction effects between explicit and implicit mechanisms; impairment of the declarative component led to performance improvements in the nondeclarative component. These findings suggest that the acquisition of declarative and procedural knowledge may not occur entirely independently of each other. In the present study we found no evidence for such influence as there was no correlation between the performance of declarative recall and skill-specific improvements.

In humans, the basolateral amygdala (BLA) is important in facilitating hippocampus - dependent explicit memory (McGaugh, 2004; Phelps, 2004; Labar & Cabeza, 2006). Studies with animals and humans point to the hippocampus and adjacent medial temporal lobe (MTL) playing a crucial role in the retrieval of sequence information. Rats with hippocampal lesions

have difficulty remembering the serial order of the sequence (Hoang & Kesner, 2008; Lee, Jerman, & Kesner, 2005). Lehn and colleagues (2009) let subjects watch a novel movie and later, during functional magnetic resonance imaging, asked them to reconstruct the temporal order of life-like events, derived from a movie they had watched the day before. Extensive MTL activation was observed during sequence recall. In another study (Paz et al., 2010) neuronal activity in hippocampus predicted the subjects' ability to recall the temporal order of cinematic episodes. Clark and Squire (1998) have shown that the MTL is necessary for conscious awareness of stimulus and task relationships. The awareness of what is learned depends on hippocampus-dependent, declarative memory (Smith, Hopkins, & Squire, 2006). By using functional MRI, Kensinger and Corkin (2004) have found that emotional memory enhancement for arousing information occurs automatically, and is mediated by an amygdalar–hippocampal network. Emotional modulation of explicit awareness of the sequence likely indicates that the task has challenged an amygdalar–hippocampal network.

In rodents, BLA is involved in modulating the consolidation of certain procedural memories. Tasks in which such evidence has been demonstrated include inhibitory avoidance (Roozendaal, Quervain, Ferry, Setlow, & McGaugh, 2001; Setlow, Roozendaal, & McGaugh, 2000; LaLumiere, Nguyen, & McGaugh, 2004; LaLumiere, Nawar, & McGaugh, 2005), conditioned taste aversion (Miranda, LaLumiere, Buen, Bermudez-Rattoni, & McGaugh, 2003), contextual fear conditioning (LaLumiere, Buen, & McGaugh, 2003), fear conditioning (Pezze, Feldon, & Murphy, 2002), auditory-cue classical fear conditioning (Roozendaal et al., 2006), reward-seeking behaviour (Ambroggi, Ishikawa, Fields, & Nicola, 2008) and conditioned place preference (Everitt, Morris, O'Brien, & Robbins, 1991). The question arises why emotional stimuli were unable to modulate skill acquisition in the SRTT, if BLA, a major neural processing node of emotions, is involved in procedural memory in animals,. One possibility would be that, although the emotional stimuli turned out to be clearly discernible, they were too weak on the whole to evoke a corresponding emotion in the participants. We

consider this possibility unlikely since similar stimuli have been shown to induce effectively corresponding emotional states in previous studies (Halberstadt & Niedenthal, 1997). Furthermore, as mentioned above, emotional stimulation was able to modulate explicit sequence recall testifying to their power to induce behaviourally significant consequences. A possible answer, then, might be provided by considering the functional anatomy of sequence learning. According to an influential model of motor sequence memory consolidation skilled behaviour in the SRTT depends on neural changes in the striatum and its associated motor cortical regions (Doyon & Benali, 2005). The striatum is divided into functional domains based on inputs from discrete brain regions. The ventral striatum receives direct and dense projections from the BLA (Sah, Faber, Lopez De Armentia, & Power, 2003; Cardinal, Parkinson, Hall & Everitt, 2002; Bouwmeester, Wolterink, & van Ree, 2002; French, Hailstone, & Totterdell, 2003; Mcdonald, 1991; Gray, 1999; Wright, Beijer, & Groenewegen, 1996; Alheid, 2003; Johnson, Aylward, Hussain, & Totterdell, 1994; Groenewegen, Wright, & Beijer, 1996). Through this route, emotional information can reach the motor system and thereby influence behavioural output (Lau & Salzman, 2009). However, sequence learning in humans has been shown to specifically engage the dorsal striatum, during learning (Jenkins, Brooks, Nixon, Frackowiak, & Passingham, 1994; Jueptner, Frith, Brooks, Frackowiak, Passingham, 1997; Aldridge & Berridge, 1998; Kermadi & Joseph, 1995; Nakamura et al., 2001; Bailey & Mair, 2006, Lehéricy et al., 2005; Poldrack et al., 2005; Yin, 2010), and post-training, during its consolidation (Doyon et al., 2002, Doyon, Penhune, & Ungerleider, 2003; Hazeltine, Grafton, & Ivry, 1997; Miyachi, Hikosaka, Miyashita, Karadi, & Rand, 1997; Miyachi, Hikosaka, & Lu, 2002; Lehéricy et al., 2005; Hikosaka et al., 1999). While the dorsal striatum receives convergent inputs from several cortical regions, including the motor and primary sensory cortex (Divac, Fonnum, & Storm-Mathisen, 1977; McGeer, McGeer, Scherer, & Singh, 1977; Donoghue & Herkenham, 1986), it is less densely connected with the BLA (Gray, 1999; Groenewegen, 2003; Groenewegen & Trimble, 2007). Against this

background, we suggest that the lack of significant influence of emotions on skill-specific changes in SRTT on one hand, and the enhanced awareness of the hidden sequence after negative emotional intervention, on the other hand, may reflect the functional dichotomy of anatomical circuits underlying memory consolidation mechanisms and processing of emotions. According to this idea, failure of emotional valence to modulate consolidation of SRTT skill is related to the absence of strong amygdalo-dorsal striatal projections, whereas enhanced declarative knowledge was due to the fact that emotional information reaches the hippocampal-based memory circuits.

Subjects' awareness of a hidden sequence was enhanced by negative emotional stimuli applied directly after learning. Since the subjects rated negative stimuli as more arousing than neutral and positive ones, the effect of valence is confounded by the effect of arousal. Some recent studies investigating effects of emotion on explicit memory revealed similar effects of arousal. Memory enhancement is most likely to occur for neutral items that precede emotionally arousing items, and are tested after a delay period of one week (Knight & Mather, 2009). Andersen and co-workers (Anderson et al., 2006) asked subjects to view pictures of neutral faces or houses preceding arousing or neutral stimuli. After 1-week delay recognition memory for neutral events was tested. The results revealed memory benefits for neutral scenes followed by arousing stimuli. Nielson and Powless (2007) also demonstrated that arousal plays a crucial role in modulation of memory consolidation. Participants saw positively or negatively arousing video clips after learning a word list. Arousal of either valence induced memory improvements in a one week later recognition test. A recent study (Judde & Rickard, 2010) using arousing musical stimuli produced similar effects. Arousal, irrespective of valence facilitated long term memory for a word list. Based on these studies, we consider it likely that explicit processes are modulated by arousing emotional stimuli. It should be noted that in our study subjects have rated negative stimuli as more arousing than neutral and positive ones. Although there is a tendency that unpleasant pictures are more

arousing than pleasant ones (Lang et al., 2005), future studies with different emotional stimuli should examine the role of arousing positive stimuli in modulation of motor learning to disentangle valence effects from arousal effects more clearly.

A recent study (Javadi et al., 2010) examined the impact of different emotional contexts during encoding on the subsequent offline consolidation of procedural learning. Participants who learned a mirror tracing skill with a negative image in the background showed greater enhancement of this skill across a retention interval than participants who trained with neutral or positive images in the background. Although mirror tracing and SRTT challenge partly different neuronal networks (Gabrieli et al., 1997; Laforce & Doyon, 2001) the findings by Javadi and co-workers (2010) suggest that emotional states may have a stronger impact on motor skill consolidation when evoked during the acquisition of a new skill than after the training experience.

In the present study we aimed to investigate the effects of emotion on memory consolidation of an SRTT skill. Our findings show that emotional interference, as done by exposing subjects to emotional visual and auditory stimuli, did not have an influence on consolidating the acquisition of an SRTT task, while negative arousing emotional stimuli enhanced the explicit awareness of sequence knowledge. Based on these findings we suggest that different mechanisms might be responsible for implicit and explicit aspects of consolidation of sequence learning. Since skill performance was not correlated with explicit awareness, we conclude that explicit and implicit modes of SRTT performance are not complementary, but rather diverse processes.

Experiment 3 -The motor side of emotions: Investigating the relationship between hemispheres, motor reactions and emotional stimuli

Introduction

Emotions are often seen as events that only describe subjective feelings of an individual. Yet, there is various evidence that emotions may be traced back to primordial reaction types like approach-appetitive, consumption-oriented, or withdrawal-avoidant, directed at minimizing unfavourable input (Lang et al., 1990). Given this perspective, positive emotions are associated with movements towards a desirable stimulus. A bodily response that is closely associated with approach is the contraction of the arm flexor which is involved in pulling an object closer to the self. Contrary, negative emotions likely relate to a movement away from an aversive source and seem to be coupled with the contraction of the arm extensor to push an object away from the self. Several studies have indeed shown that responses using flexor or extensor muscles are associated with a response bias towards pleasant or unpleasant emotional stimuli, respectively (Chen & Bargh, 1999; Coombes et al. 2007; Duckworth, Bargh, Garcia, & Chaiken, 2002; Solarz, 1960; Rotteveel & Phaf, 2004; Wentura, Rothermund, & Bak, 2000).

Another frequently investigated issue in neuropsychology and affective neuroscience is whether, and how, emotional processes are functionally lateralized across the hemispheres (Canli, 1999; Demaree et al., 2005). Two main different theories have been proposed. The first one is the “right hemisphere hypothesis”. It posits that emotional processing of both positive and negative emotions is lateralized towards the right hemisphere (Borod, 1992; Borod, Bloom, Brickman, Nakhutina, & Curko, 2002). Numerous studies have supported this hypothesis (Borod, Kent, Koff, Martin, & Alpert, 1988; Christman & Hackworth, 1993; Hugdahl, Iversen, & Johnsen, 1993; McLaren & Bryson, 1987; Moreno, Borod, Welkowitz,

& Alpert, 1990; Tamietto, Latini Corazzini, de Gelder, & Geminiani, 2006). The second theory is the "valence hypothesis" which states that hemispheres differ according to emotional valence with the right brain dominant for the processing of negative, and the left brain dominant for the processing of positive emotions (Davidson, 1995; Silberman & Weingartner, 1986). Evidence for this theory has also been supported by several studies (Ahern & Schwartz, 1985; Canli, Desmond, Zhao, Glover, & Gabrieli, 1998; Davidson et al., 1990; Jansari, Tranel, & Adolphs, 2000; Jones & Fox, 1992; Pauli, Wiedemann, & Nickola, 1999; Reuter-Lorenz & Davidson, 1981; Wiedemann et al., 1999).

Some recent studies with brain-damaged patients have supported the right hemisphere hypothesis: patients with lesions to the right hemisphere have greater impairment in the perception of emotional faces, regardless of the valence of the expressed emotion (Adolphs, Damasio, Tranel, Cooper, & Damasio, 2000; Borod et al., 1998; Bowers, Bauer, Coslett, & Heilman, 1985). Nevertheless, other studies have also provided support for the valence hypothesis: unilateral brain damage to the right hemisphere impaired the perception of negative emotions while the perception of positive ones was preserved (Adolphs, Damasio, Tranel, & Damasio, 1996; Adolphs, Jansari, & Tranel, 2001).

The assumption of strong relations between specific emotions (positive/negative) and specific motor behaviour (approach/avoidance), and the concept of specific emotions being connected to specific cerebral hemispheres, leads to the question whether there is a relationship between motor behaviour and hemispheres. In a recent study, Maxwell and Davidson (2007) have shown that flexion and extension responses are asymmetrically represented across the cerebral hemispheres with flexion responses being associated with the left hemisphere (LH) and extension responses with the right hemisphere (RH). In this reaction time experiment a participant was required to point a finger in response to the direction of a flashed arrow appearing either in the left or the right visual field and pointing away

(extension) or towards (flexion) the subject. Facilitation of flexor responses relative to extensor responses was greater in the LH than in the RH, while facilitation of extensor responses relative to flexor responses was greater in the RH than in the LH. This pattern of hemispheric specialization was observed to a greater degree with participants that evinced a higher self-reported level of daily positive affect (according to PANAS; Watson, Clark, & Tellegen, 1988) and a lower self-reported level of dispositional anxiety (according to STAI_X2; Spielberger & Diaz-Guerrero, 1983).

Based on the above mentioned studies, we aimed to answer the question whether flexion and extension responses towards positive or negative emotional pictures would bias motor processing towards the LH and RH in a similar manner as shown by Maxwell and Davidson (2007). Contrary to Maxwell and Davidson (2007), who induced flexion and extension responses by simple finger responses, we designed an experiment where flexion and extension responses had to be executed via arm movements with a joystick in order to use a more naturalistic response of approach and avoidance. In addition, we used emotional stimuli to possibly reveal a triple interaction between valence, hemifield, and response type. Driven by previous evidence we predicted faster flexion responses to positive stimuli and faster extensions to negative stimuli. We also expected a hemispheric asymmetry for this mapping between valence and motor behaviour, so that faster flexions to positive stimuli would be mediated by the left hemisphere, while the right hemisphere would dominate faster extensions to negative stimuli.

Methods

Participants

Thirty neurologically healthy subjects (15 women, 15 men, aged 19-39 years) participated in this study. The mean age of the women was 25.07 years (S.D. = 5.35, range: 19–39 years) and that of the men was 27.87 years (S.D. = 4.16, range: 20–37 years). All participants were right handed, as determined by the Edinburgh Handedness Inventory (Oldfield, 1971). The laterality-index (LQ) provided by this test is calculated by LQ= $[(R-L)/(R+L)] \times 100$, resulting in values between −100 and +100. Positive values indicate a preference for the right hand, while negative values indicate left handedness. Women had a mean LQ of 92.48 (S.D. =12.35, range: 63.63–100), while the mean LQ for men was 93.59 (S.D. =10.26, range: 68.42–100). All subjects were students recruited from the University of Bochum, Germany. They all gave written consent for participating in the experiment. Each subject in the experiment received a certificate stating the hours they had spent as test subjects (as required for their studies). The study was approved by the ethics committee of the Medical Faculty at the University of Bochum.

Affective Stimuli

The emotional pictures were taken from the International Affective Picture System (IAPS; Lang et al. 2005). Of these, we chose 40 pleasant (positive) and 40 unpleasant (negative) scenes. Positive pictures included erotic couples and happy families; negative pictures included mutilated bodies and scenes of attack and threat [3]. The pictures were selected on the basis of their mean normative ratings of valence and arousal (Lang et al., 2005) with positive and negative pictures differing in valence (positive: 7.3, negative: 2.5) but not in arousal (positive: 6.3, negative: 5.6).

[3] The numbers of IAPS pictures used were as follows. Positive: 2040, 2050, 2057, 2058, 2070, 2071,2080,2260,2660, 1710, 1440, 1441, 2150, 1920, 2091, 2332, 2311, 2345, 2344 ,2153, 4607, 4608, 4643, 4652, 4656, 4658, 4659, 4660, 4680, 4670, 4676, 4677, 4681, 4683, 4687, 4689, 4694, 4695, 4800, 4810. Negative: 6555, 6200, 6244, 6213,6250, 6550, 6300, 6570.1, 6510, 6230, 6212, 6540, 2811, 6560, 6313, 6350, 1930,1300, 1301, 2120, 3000, 3010, 9435, 6021, 6022, 3016, 3062, 9433,2800, 3069, 3005.1, 3015,3063, 1113, 1120, 1201, 1052, 1050, 1111, 2095.

Picture Presentation

Participants were asked to place their head on a chin rest, at a distance of approximately 57 cm from a monitor, so that 1 cm represents 1◦ visual angle. The inner edge of the photographs was placed 4° from the central cross. To ensure that lateralized stimuli were presented more than 2° visual angle to the left or right of a central fixation cross, we instructed our participants to keep their head and body still and to fixate that cross during the whole experiment. All stimuli were presented in a frame of 11.5 cm in width and 11.5 cm in height. Each picture was presented on a 16-in. computer screen with a frame refresh rate of 75 Hz. The stimuli were presented with Presentation 12.2 software.

Motor Task and Procedure

The experiment task consisted of two conditions. In one condition positive pictures were responded to by joystick flexion (i.e. self-directed movements) and negative pictures by joystick extension (i.e. movements directed away from the self); in the second condition these relations were inversed, negative pictures were responded to by joystick flexion (i.e. self-directed movements) and positive pictures by joystick extension (i.e. movements directed away from the self). Participants had to respond as quickly and as correctly as possible.

Each participant completed both task conditions with 800 test trials each. Task conditions were separated by a 15 min. break and started with 40 practice trials. Within each task condition, each picture was presented 10 times in a randomized order. The order of task condition and hand use was balanced using a randomized block design. Within each condition, the responding hand was changed after 400 trials.

Each trial began with the presentation of a central fixation cross presented for 1000 ms. Then the lateralized picture appeared randomly either in the left or the right visual hemifield for 180 ms. Participants were instructed to respond as fast and as accurately as

possible. After their response, the subjects had to move back the joystick into start position, from there next trial started immediately.

Data analysis

Reaction time was recorded with Presentation 12.2 software. For statistical analysis of the behavioural data, SPSS Statistics 17 for Windows (SPSS Inc., Chicago, IL) was used. For both task conditions, we measured the median reaction time of all responses for each subject differentiated for the experimental conditions. Median reaction times were analyzed with a mixed 2x2x2 ANOVA with response type (flexion, extension), valence (positive, negative) and hemifield (RVH, LVH) as within-subjects factors. The assumption of normality for each condition was tested using the Kolmogorov-Smirnov test. The results of these tests showed that the data for all conditions were normally distributed (all p's >0.05) Thus, no significant deviation from normality was observed.

Results

The reactions to stimuli presented in the left hemifield (Mean = 477.50 ms; S.D= 11.06 ms) were overall faster than in the right hemifield (Mean = 482.17 ms; S.D= 11.89).

The significant interaction of hemifield and valence [F (1, 29) = 9.890, p=0.004] further indicated that this effect was modulated by the pictures valence. Participants responded faster to negative stimuli presented in the left visual hemifield (LVH) than in the RVH (paired t-test, p=0.001) whereas no such differences in reaction times between left and right visual hemifield were observed for positive stimuli (paired t-test, p=0.936). The responses to negative stimuli presented in the right hemifield were not statistically different from those to positive stimuli presented in the right hemifield (paired t-test, p=0.074). Also responses to positive stimuli presented in the left hemifield did not differ statistically from responses to negative stimuli presented in the left hemifield (paired t-test, p=0.709) (see Figure 9).

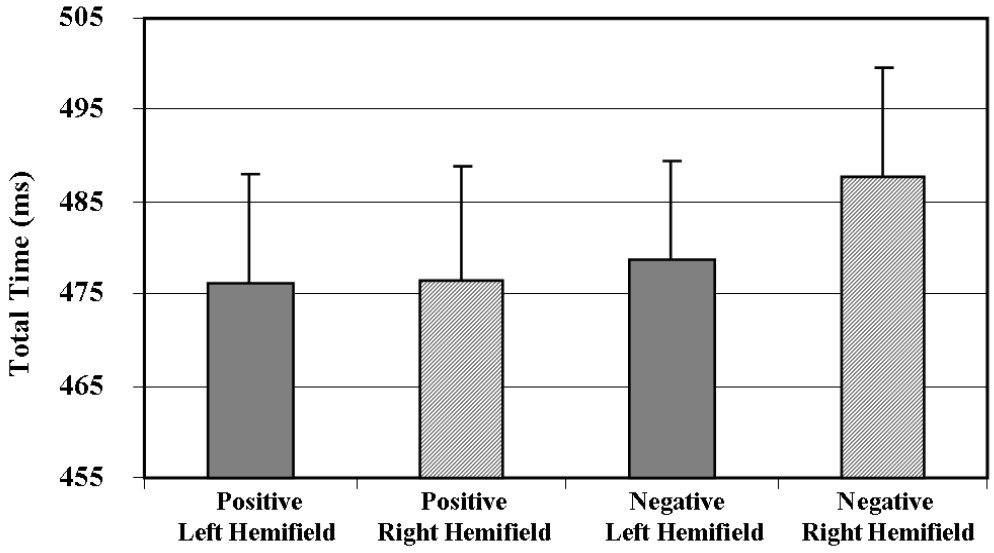

Figure 9. Average Median Reaction Times (ms) of both extension and flexion responses for both positive and negative emotional stimuli. Error bars show standard deviation.

As shown by a significant interaction of valence and response type, [F (1, 29) = 6.335, p= 0.018] responses to positive stimuli were faster in the flexion condition than in the extension condition (paired t-test, p=0.006), whereas responses to negative stimuli were faster in the extension condition than in the flexion condition (paired t-test, p= 0.001), (see Figure 10).

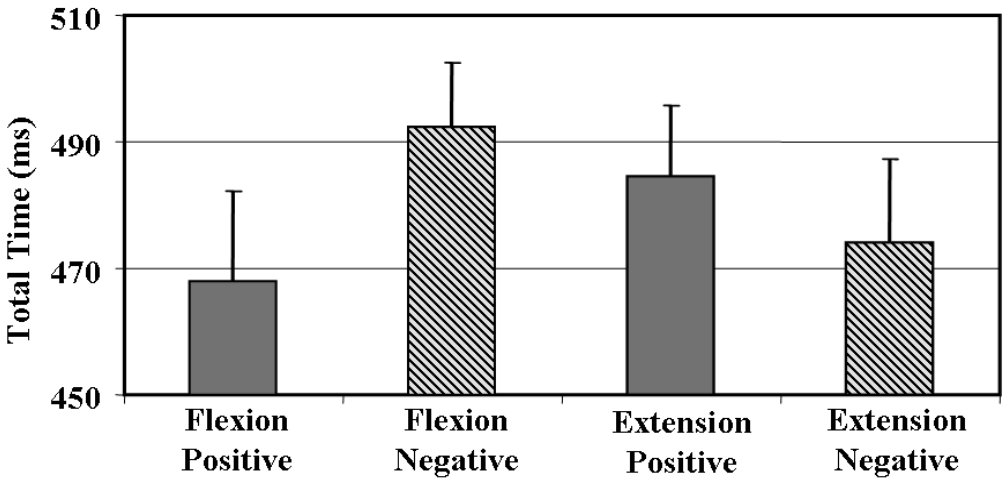

Figure 10. Average Median Reaction Times (ms) of all responses for both positive and negative emotional stimuli in both right and left hemifields. Error bars show standard deviation.

There were no significant double (response type, hemifield) ($F < 1$) or triple (response type, hemifield, valence) ($F < 1$) interactions.

Discussion

We have investigated if motor response patterns, i.e. arm flexion versus extension, are associated with a lateralized organization of emotions. Corroborating previous studies (e.g., Chen & Bargh, 1999; Duckworth et al., 2002) we observed that flexion responses were faster to positive stimuli, while negative stimuli were associated with faster extension responses. Importantly, we also observed that reactions were overall faster for emotional stimuli presented in the left visual hemifield. However, this effect was further modulated by the valence of the stimuli, with only negative photographs presented in the LVH eliciting faster responses compared to RVH presentations. Finally, we could not reveal an interaction between response type and hemifield. Thus, we found no evidence for a predominance of speeded flexion responses from the left hemisphere and extensor responses from the right one. Neither was there any triple interaction between valence, hemifield, and response type. Hence, a predominance of speeded flexion responses towards positive stimuli from the left hemisphere, and extensor responses to negative pictures from the right one, could not be shown. We are going to discuss these points, one by one.

In line with previous studies (Chen & Bargh, 1999; Coombes et al., 2007; Duckworth et al., 2002; Solarz, 1960; Rotteveel & Phaf, 2004) our results showed that flexion and extension responses are associated with positive and negative stimuli, respectively. The application of various stimulus types has hitherto shown this association between the direction of a motor response and a bidirectional stimulus valence. This has been revealed for valenced words (Chen & Bargh, 1999), abstract images (Duckworth et al., 2002), facial expressions (Marsh, Kleck, & Ambady, 2005), object pictures (Lavender & Hommel, 2007), and phobic objects (Rinck & Becker, 2007). The vast majority of these experiments utilized arm movements. Finger movements (Maxwell & Davidson, 2007), and button presses (Wentura et al., 2000) were also employed. Thus, our data meet with plenty of support from the literature,

making it likely that the approach to a desired target and the avoidance of agonistic stimuli are evolutionarily coded by prefixed movement patterns. According to a recent study (Van Dantzig, Pecher, & Zwaan, 2008), however, there are two ways of grabbing the desired object: pulling this object towards the self (flexion movement) or reaching out towards the target (extension movement). Thus, the same motivational background can principally control two diverse motor patterns. Wentura et al. (2000) have in fact recorded faster push movements to positive stimuli with button presses resulting in a decrease in the distance between oneself and the target, whereas pull movements to negative stimuli were faster with button releases increasing the distance. Similarly, Van Dantzig et al. (2008) were able to link neutral key presses with negative or positive stimulus movements, towards or away from the participant, and still their findings showed that responses were fastest when positive or negative words were directed towards, or away, from the subject. Therefore, the association of flexion (positive) and extension (negative) appears to be the emerging default mode so frequently encountered in many studies, including the present one. However, if associated with reverse outcome (flexion followed by approach of negative stimuli; extension followed by disappearance of positive stimuli) a rapid remapping of this valence-motor connection is possible.

Our results showed that reaction times for emotional stimuli presented in the LVH were overall faster than for stimuli presented in the right hemifield. This result is consistent with the right hemisphere hypothesis which posits that this brain half is characterized by an overall superiority for emotional cues, independent of their valence (Alves, Aznar-Casanova, & Fukusima, 2009; Christman & Hackworth, 1993; Dimberg & Petterson, 2000; Hugdahl et al., 1993; McLaren & Bryson, 1987; Moreno et al., 1990; Narumoto, Okada, Sadato, Fukui, & Yonekura, 2001; Rodway & Schepman, 2007; Sato, Kochiyama, Yoshikawa, Naito, & Matsumura, 2004; Tamietto et al., 2006). However, if these results are differentiated according to valence and visual hemifield, the overall pattern changes. Now it turns out that

responses to negative emotional cues were faster in the LVH, but that responses to positive emotional cues were almost equal in both hemifields. Thus, our results support a mixed pattern of valence and right hemisphere hypotheses. On the one hand, they confirm an overall specialization of the right hemisphere in processing emotion. On the other hand, they show a difference for negative pictures with a higher involvement of the right hemisphere, resulting in an even impact of left- and right-hemisphere processes when presenting positive pictures.

Our pattern of results resembles a large number of different studies that show a right hemispheric specialization for negative affect and a bihemispheric processing of positive valence issues (Adolphs et al., 2001; Asthana & Mandal, 2001; Kensinger & Choi, 2009; Killgore & Yurgelun-Todd, 2007; Kimura, Yoshino, Takahashi, & Nomura, 2004; Mandal, Tandon, & Asthana, 1991; Natale, Gur,& Gur, 1983; Noesselt, Driver, Heinzel, & Dolan, 2005; Sato & Aoki, 2006; Simon-Thomas, Role, & Knight, 2005; Smith & Bulman-Fleming, 2004). Therefore, a multitude of different approaches reveal a differential architecture of emotional processes between the hemispheres. Neither do we seem to have a simple dominance pattern for an overall processing of emotions. Nor are negative and positive affects simply mapped in a complementary way onto the two hemispheres.

Our results support the assumption that both hemispheres associated fast flexion responses to positive and fast extensions to negative emotional stimuli. This mapping of motor directions to stimulus valence was independent of the hemispheres. This pattern is to some extent in contradiction with several previous studies. Maxwell and Davidson (2007) revealed a differential lateralization of finger flexion and extension actions which were associated with left hemispheric flexion and right hemispheric extension responses, respectively. Cretenet and Dru (2004) devised an experimental approach that tested this concordance of movement direction, valence, and side in a more indirect way. In their study, subjects had to judge neutral stimuli while performing unilateral movements with both arms.

They showed that right-arm flexion together with left-arm extension shifted evaluations towards positive values; while the opposite arm movements resulted in negative judgements. The authors invoked a motor congruence model to describe their results. Accordingly, left arm extension and right arm flexion are perceived as a congruent condition, resulting in positive judgements, whereas the opposite pattern is seen as non-congruent and triggers negative evaluations. Later they could replicate and extend this result and further revealed that neutral judgements are determined by bilateral flexion or bilateral extension (Dru & Cretenet, 2005). In a recent study (Dru & Cretenet, 2008) participants judged valenced stimuli according to the motor congruence model. Negative stimuli were evaluated less negatively when a non-congruent unilateral motor behaviour was performed, and more negatively while performing a congruent motor behaviour. On the other hand, positive stimuli were evaluated less positive when a non-congruent unilateral motor behaviour was performed, and more positive when a congruent unilateral motor behaviour was performed.

Schiff and Bassel (1996) showed that unilateral facial contractions differentially influenced the reaction time of finger flexion (approach) and finger extension (withdrawal) responses but had no effect on the participants' self-rating of mood. Left-sided facial contractions (right hemisphere activated) facilitated finger extension and retarded the flexion response with the left hand. Right-sided facial contractions (left hemisphere), however, facilitated finger flexion and retarded the finger extension response with the right hand. In an earlier study (Sobotka, Davidson, & Senulis, 1992), subjects reacted to target stimuli (reward or punishment contingencies) by applying either an approach (finger press) or a withdrawal response (finger lift). Reward trials were associated with greater left-sided frontal activity, while punishment trials were associated with greater right-sided frontal activity. Contrary to the prediction there was no significant interaction of movement and hemisphere in the frontal regions, though withdrawal or approach responses were linked with greater right- or left-sided temporo-parietal activations, respectively.

A similar asymmetry pattern with an appetitive specialization of the left, and an aversion-related dominance of the right hemisphere has been observed in various animal species. Different species of birds show a rightward bias for feeding responses (zebrafinches: Alonso, 1998; chicks: Dharmaretnam & Rogers, 2005; pigeons: Güntürkün, 1997; Güntürkün & Kesch, 1987; Vallortigara, Regolin, Bortolomiol, & Tommasi, 1996; quails: Valenti, Sovrano, Zucca, & Vallortigara, 2003; black-winged stilts: Ventolini et al., 2005). This is also similar in toads that show a right hemifield preference for directing tongue strikes at prey (Robins & Rogers, 2004), while faster responses to predators approaching from the left have been found in chicks (Evans, Evans, & Marler, 1993), toads (Lippolis, Bisazza, Rogers, & Vallortigara, 2002), and fish (De Santi, Sovrano, Bisazza, & Vallortigara, 2001). If we assume that positive emotional cues within the human domain are comparable to food-items and that negative cues are an analogy to predators, then the results from the human and the non-human literature are congruent. Thus, an overarching picture of a left hemispheric approach system for positive, and a right hemispheric avoidance system for negative stimuli should be the overall vertebrate condition. However, our results do not support such a triple interaction between response type, hemifield and valence. It is always difficult to interpret negative data, and we are therefore cautious with our following statements.

It becomes clear why we couldn't observe this when looking at the finding that both flexion and extension responses to negative stimuli are fastest when presented in the LVH, while such a similar laterality effect could not be seen for positive ones. In interaction of that kind, the interaction effect between valence and hemifield seems to be stronger than the interaction effect between valence and response type, as the right hemisphere responds faster to negative stimuli (in comparison to the left hemisphere), independent of either flexion or extension occurring. The right hemisphere specialisation in negative valence therefore seems to be stronger than its lateralization for motor behaviour. Similar observations can be made regarding positive stimuli. It is because of the bihemispheric processing of positive valence

that both hemispheres show almost the same speed in extensions and flexions to positive stimuli.

Still, we would like to emphasize that our approach differs to some extent from previous ones. First, in contrast to some of the cited studies (Sobotka et al., 1992; Schiff & Bassel, 1996; Maxwell & Davidson, 2007), we included an overt emotional manipulation and additionally required our subjects to perform full arm and not mere finger movements. Second, different to Dru and Cretenet (2005, 2008; Cretenet & Dru, 2004) we did not analyze alterations in stimulus judgements but reaction times after emotional stimulus presentations. Thus, we devised our experiment as being relatively close to a possible evolutionary scenario in which appetitive or aversive stimuli are to be responded to by means of movements that either drag them towards the subject or push them away.

It should also be noted that in our study the predominant role of the right hemisphere in processing emotions might also be due to the RH`s role in identifying visual stimuli. According to Kosslyn and colleagues, analyzing subtle spatial and physical cues that allow us to identify visual objects may preferentially occur in the RH (Kosslyn, 1987; Kosslyn et al., 1989). Another feature of RH is its specialization for attention. The left hemisphere attends to contralateral stimuli whereas the right attends to both contralateral and ipsilateral stimuli (Heilman & Van den Abell, 1980). Future studies should examine whether our results can be replicated with different stimulus modalities. For example, a recent meta-analysis study (Murphy, Nimmo-Smith, & Lawrence, 2003) could not show a dominant role of the right hemisphere in emotion perception when a wider range of stimulus modalities was considered (visual, auditory, olfactory, tactile, and taste).

At the neural level, it seems to be important whether an emotional stimulus is positive or negative. If it is negative, the brain will respond more dominantly with the right hemisphere, whereas a positive stimulus entails a response in both hemispheres. This

ostensibly selective specialization, however, does not mean that there are no other asymmetries. Rather, one would assume that under certain conditions a hierarchy scaling of the asymmetry patterns prevails. Wherever an immediate reaction to the stimulus is enforced, as was our experimental prerequisite, a predominance of the paramount vital functions appears. Under other conditions, which also allow delayed responses, other functionalities, and therefore asymmetries, should become visible. This might have been masked by the hierarchy scaling in our context.

General Discussion

This dissertation aimed to investigate if and how emotions may affect motor memory processes. In three different experiments the influence of emotional interference was investigated by modulating three different motor memory processes: encoding of motor memory, consolidation of motor memory, and learning of associations between emotional cues and motor responses.

In the first experiment subjects were exposed to emotional interference during encoding of a motor skill. The results showed best performances for motor learning in the negative valence-low arousal condition. Since this enhancement was not significantly better in comparison to other emotional conditions, we are unable to draw firm conclusions. On the other hand emotional induction was not efficient in one experimental condition: the arousal ratings of positive valence-low arousal condition were not significantly lower than positive valence-high arousal and negative valence-high arousal conditions. This points to a fundamental issue in experiments with valence-arousal interactions. Conditions that trigger positive affect tend to enhance arousal. It is widely accepted that they raise – like arousal – the level of particular cerebral neuromodulators (Ashby, Valentin, & Turken, 2002). Contrariwise, some arousing events induce a positive mood in humans, although they are normally perceived as negative incidents, as exemplified by bungee jumping. It is therefore potentially difficult to determine to what degree the induction of valence or arousal is affected by the linking of stimulus to context (presentation/task) or whether it is affected by individual disposition. While we cannot rule out that the problem with emotional induction was solely because of its inefficiency, it would be beneficial to control such tendencies in subject's appraisals of emotions in future experiments, for example by administrating trait-anxiety scales. Despite the fact that our results fall short of providing unequivocal bases for conclusion, they do possibly show a trend to be pursued and explored in future.

Next we could, though admittedly in a merely speculative capacity, conjecture that in contrast to explicit memory processes, by which memory-enhancing effects of emotion mostly depend on rising arousal, implicit memory enhancements might be particularly pronounced for events that elicit negative valence with small increases in arousal. This assumption partially fits in with the well-known Yerkes-Dodson (1908) effect, according to which small and moderate increases in arousal improve performance, whereas a transgression of the ideal value in arousal results in a disruptive effect. Since, in our experiment, the negative valence-high arousal condition did not induce high arousal in our subjects, we cannot infer any consequences about detrimental effects of such a condition. Further experimental designs testing if emotions can modulate motor encoding processes, should therefore use different negative emotional stimuli, which have to be able to induce the deserved valence-arousal interactions in an efficient manner.

In summary, it can be said that, in spite of a missing significance of results, further research questions and systematic approaches have been brought to attention, and these are worthy of continuing investigation.

Based on the findings of the second experiment we suggested that different mechanisms might be responsible for implicit and explicit aspects of consolidation of sequence learning. The lack of significant influence of emotions on skill-specific changes in SRTT on the one hand, and the enhanced awareness of the hidden sequence after negative emotional intervention, on the other hand, may reflect a functional dichotomy of anatomical emotion processing circuits underlying memory consolidation mechanisms These results should be confirmed by using brain imaging techniques. Especially, it should be investigated how emotional exposure affects explicit aspects of SRTT skill consolidation. In addition, it should be tested if emotion would indeed not affect brain circuits which are responsible for implicit aspects.

It is important to note that we have to refrain from concluding that consolidation cannot be modulated by emotions for all motor tasks. Experimental settings with different emotional stimuli and different motor tasks would help us determine the borders of emotional effects on motor memory consolidation. Likewise, the application of different time intervals, both for post-testing and emotional interference, could help us observe how the pattern of findings would change. In the light of our results we can say, emotions very likely do not affect implicit motor consolidation of SRTT skill. But since most of our daily cognitive abilities are based on sequence learning, a skill which is insensitive to emotional modulation may, if seen from an evolutionary point of view, be entirely functional and turn out to be conducive to survival.

In our last experiment we did not observe any interaction between hemifield and response type, nor any triple interaction between hemifield, response and emotion. We assume that the relations between these three actors are masked by a special characteristic of the brain, which is capable of processing in a hierarchical system. Wherever an immediate reaction to the stimulus is enforced, as was our experimental prerequisite, a predominance of the paramount vital functions appears. In other words, the results clearly bring us to see how the brain is able to bias its motor reactions in an evaluative manner. This assumption is interesting for future experiments investigating double or triple interactions concerning emotional processing and motor learning processes. The priority of brain choices in response selection can be modulated by different experimental settings. As a consequence, the hierarchy scaling of interactions can change. Thus, we might not only influence the response repertoire of the brain by modulating experimental conditions, we can also understand emotion-related motor reactions from a different point of view.

In brief, the results have evinced a different perspective in research of emotion related motor behaviour. In special experimental conditions the brain can open its magic box, mimicking its preferences for motor reactions. Future experiments should explore if similar or

different interaction patterns would emerge by applying different emotional stimuli. In a more natural experimental context, these patterns can be investigated, for example in a computer game in which responses require innate motor behaviours like avoidance or approach.

To sum up, there are a lot of questions to be answered to better understand the relations between emotion and motor learning. This dissertation is a further step in the big picture of emotion and its effects on motor memory processes. More research will be needed for clear and distinct conclusions.

References

Adolphs, R., Damasio, H., Tranel, D., & Damasio, A. R. (1996). Cortical systems for the recognition of emotion in facial expressions. *The Journal of Neuroscience, 16*, 7678-7687.

Adolphs, R., Damasio, H., Tranel. D., Cooper, G., & Damasio, A.R. (2000). A role for somatosensory cortices in the visual recognition of emotion as revealed by three-dimensional lesion mapping. *The Journal of Neuroscience, 20*, 2683-2690.

Adolphs, R., Jansari, A., & Tranel, D. (2001). Hemispheric perception of emotional valence from facial expressions. *Neuropsychology, 15*, 516–524.

Ahern, G. L., & Schwartz, G. E. (1985). Differential lateralization for positive and negative emotion in the human brain: EEG spectral analysis. *Neuropsychologia, 23*, 745-755.

Aldridge, J.W., & Berridge, K.C. (1998). Coding of serial order by neostriatal neurons: a "natural action" approach to movement sequence. *The Journal of Neuroscience, 18,* 2777-2787.

Alonso, Y. (1998). Lateralization of visual guided behavior during feeding in zebra finches (Taeniopygia guttata). *Behavioral Processes, 43*, 257–263.

Alheid, G.F. (2003). Extended amygdala and basal forebrain. Annals of the New York *Academy of Sciences, 985,* 185-205.

Alves, N. T., Aznar-Casanova, J. A., & Fukusima, S. S. (2009). Patterns of brain asymmetry in the perception of positive and negative facial expressions. *Laterity, 14*, 256-272.

Ambroggi, F., Ishikawa, A., Fields, H.L., & Nicola, S.M. (2008). Basolateral Amygdala Neurons Facilitate Reward-Seeking Behavior by Exciting Nucleus Accumbens Neurons. *Neuron, 59,* 648-661.

Anderson, A.K., Christoff, K., Stappen, I., Panitz, D., Ghahremani, D.G., Glover, G., Gabrieli, J.D., & Sobel, N. (2003). Dissociated neural representations of intensity and valence in human olfaction. *Nature Neuroscience, 6,* 196-202.

Anderson, A.K., Wais, P.E., & Gabrieli, J.D. (2006). Emotion enhances remembrance of neutral events past. *Proceedings of the National Academy of Sciences, U.S.A., 103,* 1599-1604.

Andreatta, M., Mühlberger A., Yarali A., Gerber B., & Pauli, P. (2010). A rift between implicit and explicit conditioned valence in human pain relief learning. *Proceedings of the Royal Society of London Series B-biological Sciences, 277,* 2411-2416.

Apter, M. J. (1989). *Reversal theory: Motivation, emotion and personality*. London: Routedge.

Ashby, F. G., Isen, A. M, & Turken, U. (1999). A neuropsychological theory of positive affect and its influence on cognition. *Psychological Review, 106*, 529–550.

Ashby, F.G., Valentin, V.V., & Turken, A.U. (2002). The effects of positive affect and arousal on working memory and executive attention: Neurobiology and computational models. In: Moore S, Oaksford M, editors. *Emotional cognition: From brain to behavior* (pp. 245–287). Amsterdam: John Benjamins.

Asthana, H. S., & Mandal, M. K. (2001).Visual-field bias in the judgment of facial expression of emotion. *The Journal of General Psychology, 128*, 21-29.

Atkinson, R. C., & Shiffrin, R. M. (1971). The control of short term memory. *Scientific American, 225*, 82-90.

Azevedo, T.M., Volchan, E., Imbiriba, L.A., Rodrigues, E.C., Oliveira, J.M., Lutterbach, L.G. & Vargas, C.D. (2005). A freezing-like posture to pictures of mutilation. *Psychophysiology, 42*, 255-260.

Bailey, K.R., & Mair, R.G. (2006). The role of striatum in initiation and execution of learned action sequences in rats. *The Journal of Neuroscience, 26*, 1016–1025.

Baraduc, P., Lang, N., Rothwell, J.C., & Wolpert, D.M. (2004). Consolidation of dynamic motor learning is not disrupted by rTMS of primary motor cortex. *Current Biology, 14*, 252–256.

Bard, P. (1934). On emotional expression after decortication with some remarks on certain theoretical views. *Psychological Reviews, 41*, 309-329.

Baumgartner, T., Lutz, K., Schmidt, C., & Jäncke, L. (2006). The emotional power of music: How music enhances the feeling of affective pictures. *Brain Research, 1075*, 151-164.

Baumgartner, T., Willi, M., & Jäncke, L. (2007). Modulation of corticospinal activity by strong emotions evoked by pictures and classical music: a transcranial magnetic stimulation study. *Neuroreport, 18*, 261-265.

Blood, A.J., Zatorre, R.J., Bermudez, P., & Evans, A.C. (1999). Emotional responses to pleasant and unpleasant music correlate with activity in paralimbic brain regions. *Nature Neuroscience, 2*, 382–387.

Borod, J. C. (1992). Interhemispheric and intrahemispheric control of emotion: a focus on unilateral brain damage. *Journal of Consulting and Clinical Psychology, 60,* 339-348.

Borod, J. C., Kent, J., Koff, E., Martin, C., & Alpert, M. (1988). Facial asymmetry while posing positive and negative emotions: support for the right hemisphere hypothesis. *Neuropsychologia, 26,* 759-764.

Borod, J. C., Cicero, B. A., Obler, L. K., Welkowitz, J., Erhan, H. M, Santschi, C., et al. (1998). Right hemisphere emotional perception: evidence across multiple channels. *Neuropsychology, 12,* 446–458.

Borod, J. C., Bloom, R. L., Brickman, A. M., Nakhutina, L., & Curko, E. A. (2002). Emotional processing deficits in individuals with unilateral brain damage. *Applied Neuropsychology, 9,* 23-36.

Bouwmeester, H., Wolterink, G., & van Ree, J.M. (2002). Neonatal development of projections from the basolateral amygdala to prefrontal, striatal, and thalamic structures in the rat. *Journal of Comparative Neurology, 442,* 239-249.

Bowers, D., Bauer, R. M., Coslett, H. B., & Heilman, K. M. (1985). Processing of face by patients with unilateral hemisphere lesions: dissociations between judgements of facial affect and facial identity. *Brain and Cognition, 4,* 258-272.

Bradley, M. M., Greenwald, M. K., Petry, M. C., & Lang, P. J. (1992). Remembering pictures: Pleasure and arousal in memory. *Journal of Experimental Psychology. Learning, Memory, and Cognition, 18,* 379–390.

Bradley, M.M., & Lang, P.J. (1999). *International affective digitized sounds (IADS): Stimuli, instruction manual and affective ratings* (Tech. Rep. No. B-2). Gainesville, FL: The Center for Research in Psychophysiology, University of Florida.

Bradley, M. M., & Lang, P. J. (2000a). Measuring emotion: Behavior, feeling, and physiology. In R. D. Lane & L. Nadel (Eds.), *Cognitive Neuroscience of Emotion* (pp. 242-276). New York: US: Oxford University Press.

Bradley, M. M., & Lang, P. J. (2000b). Affective reactions to acoustic stimuli. *Psychophysiology, 37,* 204-215.

Bradley, B. P., Mogg, K., Falla, S. J., & Hamilton, L. R. (1998). Attentional bias for threatening facial expressions in anxiety: Manipulation of stimulus duration. *Cognition and Emotion, 12,* 737–753.

Brashers-Krug, T., Shadmehr, R, & Bizzi, E. (1996). Consolidation in human motor memory. *Nature, 382*, 252-255.

Bremner, J. D., Staib, L. H., Kaloupek, D., Southwick, S. M.,Soufer, R., & Charney, D. S. (1999). Neural correlates of exposure to traumatic pictures and sound in Vietnam combat veterans with and without posttraumatic stress disorder: A positron emission tomography study. *Biological Psychiatry, 45*, 806-816.

Brown, J. (1964). Short-term memory. *British Medical Bulletin, 20*, 8-11.

Brown, R., & Kulik, J. (1977). Flashbulb memories. *Cognition, 5*, 73-99.

Brown, R.M., & Robertson, E.M. (2007). Off-line processing: reciprocal interactions between declarative and procedural memories. *The Journal of Neuroscience, 27*, 10468-10475.

Buchanan, T. W., Etzel, J. A., Adolphs, R., & Tranel, D. (2006). The influence of autonomic arousal and semantic relatedness on memory for emotional words. *International Journal of Psychophysiology, 61*, 26–33.

Cacioppo, J. T., & Berntson, G. G. (1994). Relationship between attitudes and evaluative space; A critical review, with emphasis on the separability of positive and negative substrates. *Psychological Bulletin, 115*, 401–423.

Cahill, L., & McGaugh, J.L. (1995). A novel demonstration of enhanced memory associated with emotional arousal. *Consciousness and Cognition, 4*, 410-421.

Cahill, L., & McGaugh, J.L. (1998). Mechanisms of emotional arousal and lasting declarative memory. *Trends in Neurosciences, 21*, 294-299.

Cahill, L., Prins, B., Weber, M., & McGaugh, J. L. (1994). Beta-adrenergic activation and memory for emotional events. *Nature, 371*, 702-704.

Cajochen, C., Knoblauch, V., Wirz-Justice, A., Krauchi, K., Graw, P., & Wallach, D. (2004). Circadian modulation of sequence learning under high and low sleep pressure conditions. *Behavioural Brain Research, 151*, 167-176.

Canli, T., Desmond, J. E., Zhao, Z., Glover, G., & Gabrieli, J. D. E. (1998). Hemispheric asymmetry for emotional stimuli detected with fMRI. *Neuroreport, 9*, 3233-3239.

Canli, T. (1999). Hemispheric asymmetry in the experience of emotion: A perspective from functional imaging. *The Neuroscientist, 5*, 201-207.

Cannon, W. B. (1927). The James-Lange theory of emotion: A critical examination and an alternative theory. *American Journal of Psychology, 39*, 106-124.

Cardinal, J.A., Parkinson, J.A., Hall, J., Everitt, B.J. (2002). Emotion and motivation: the role of the amygdala, ventral striatum, and prefrontal cortex. *Neuroscience & Biobehavioral Reviews, 26*, 321-352.

Carver, C. S., & Harmon-Jones, E. (2009). Anger is an approach-related affect: evidence and implications. *Psychological Bulletin, 135*, 183-204.

Chen, M., & Bargh, J. A. (1999). Consequences of automatic evaluation: Immediate behavioral predispositions to approach or avoid the stimulus. *Personality and Social Psychology Bulletin, 25*, 215-224.

Christman, S. D., & Hackworth, M. D. (1993). Equivalent perceptual asymmetries for free viewing of positive and negative emotional expressions in chimeric faces. *Neuropsychologia, 31*, 621-624.

Clark, R.E., & Squire, L.R. (1998). Classical conditioning and brain systems: The role of awareness. *Science, 280*, 77-81.

Classen, J., Liepert, J, Wise, S.P., Hallett, M., & Cohen, L.G. (1998). Rapid plasticity of human cortical movement representation induced by practice. *Journal of Neurophysiology, 79*, 1117-1123.

Cretenet, J., & Dru, V. (2004). The influence of unilateral and bilateral arm flexion versus extension on judgments: An exploratory case of motor congruence. *Emotion, 4*, 282–294.

Coombes, S. A., Cauraugh, J. H., & Janelle, C. M. (2007). Emotional state and initiating cue alter central and peripheral motor processes. *Emotion, 7*, 275-284.

Damasio, A. R. (1994). *Descartes' error: Emotion, reason and the human brain*, New York: Grosset/Putnam.

Damasio, A.R. (1996). The somatic marker hypothesis and the possible functions of the prefrontal cortex. *Proceedings of the Royal Society of London Series B-biological Sciences, 351*, 1413–1420.

D'Argembeau, A., Comblain, C., & van der Linden, M. (2005). Affective valence and the self-reference effect: influence of retrieval conditions. *British Journal of Psychology, 96*, 457-466.

Darwin, C. (1872). *The Expression of Emotions in Man and Animals.* University of Chicago Press [reprinted (1998) (3rd edn) ed. P.Ekman. Harper Collins], Glasgow.

Davidson, R. J., Ekman, P., Saron, C. D., Senulis, J. A., & Friesen, W. V. (1990). Approach-withdrawal and cerebral asymmetry: emotional expression and brain physiology. *Journal of Personality and Social Psychology, 58,* 330-341.

Davidson, R. J. (1995). *Cerebral asymmetry, emotion, and affective style.* In R.J. Davidson & K. Hughdahl (Eds.), Brain Asymmetry (pp. 361-387). Massachusetts: MIT Press.

Demaree, H. A., Everhart, D. E., Youngstrom, E. A., & Harrison, D. W. (2005). Brain lateralization of emotional processing: Historical roots and a future incorporating "dominance". *Behavioral and Cognitive Neuroscience Reviews, 4,* 3-20.

De Santi, A., Sovrano, V. A., Bisazza, A., & Vallortigara, G. (2001). Mosquitofish display differential left- and right-eye use during mirror-image scrutiny and predator-inspection responses. *Animal Behaviour, 61,* 305–310.

Dharmaretnam, M., & Rogers L. J. (2005). Hemispheric specialization and dual processing in strongly versus weakly lateralized chicks. *Behavioural Brain Research, 162,* 62–70.

Dickinson, A., & Dearing, M. F. (1979). Appetitive-aversive interactions and inhibitory processes. In A. Dickinson & R. A. Boakes (Eds.), *Mechanisms of learning and motivation* (pp. 203-231). Hillsdale, NJ: Erlbaum.

Dimberg, U., & Petterson, M. (2000). Facial reactions to happy and angry facial expressions: Evidence for right hemisphere dominance. *Psychophysiology, 37,* 693-696.

Divac, I., Fonnum, F., & Storm-Mathisen, J. (1977). High affinity uptake of glutamate in terminals of corticostriatal axons. *Nature, 266,* 377 -378.

Donoghue, J.P., & Herkenham, M. (1986). Neostriatal projections from individual cortical fields conform to histochemically distinct striatal compartments in the rat. *Brain Research, 365,* 397-403.

Doyon, J., Song, A.W., Karni, A., Lalonde, F., Adams, M.M., & Ungerleider, L.G. (2002). Experience-dependent changes in cerebellar contributions to motor sequence learning. *Proceedings of the National Academy of Sciences, U.S.A., 99,* 1017-1022.

Doyon, J., Penhune, V., & Ungerleider, L.G. (2003). Distinct contribution of the cortico-striatal and cortico-cerebellar systems to motor skill learning. *Neuropsychologia, 41,* 252-262.

Doyon, J., & Benali, H. (2005). Reorganization and plasticity in the adult brain during learning of motor skills. *Current Opinion in Neurobiology, 15,* 161-167.

Dru, V., & Cretenet, J. (2005). Influence of bilateral motor action on judgments: Additional evidence for the motor congruence hypothesis. *Laterality, 10*, 389–398.

Dru, V., & Cretenet, J. (2008). Influence of unilateral motor behaviors on the judgment of valenced stimuli. *Cortex, 44*, 717-727.

Duckworth, K. L., Bargh, J. A., Garcia, M., & Chaiken, S. (2002). The automatic evaluation of novel stimuli. *Psychological Science, 13*, 513-519.

Ekman, P., & Friesen, W. V. (1969). The Repertoire of Nonverbal Behavior Categories, origins, usage, and coding. *Semiotica, 1*, 49- 98.

Ekman, P, & Friesen, W.V. (1971). Constants across cultures in the face and emotion. *Journal of Personality and Social Psychology, 17,* 124-129.

Erk, S., Kiefer, M., Grothe, J., Wunderlich, A.P., Spitzer, M., & Walter, H. (2003). Emotional context modulates subsequent memory effect. *Neuroimage, 18,* 439-447.

Erk, S., Martin, S., & Walter, H. (2005). Emotional context during encoding of neutral items modulates brain activation not only during encoding but also during recognition. *Neuroimage, 26,* 829-838.

Evans, C. S., Evans, L., & Marler, P. (1993). On the meaning of alarm calls: functional reference in an avian vocal system. *Animal Behaviour, 46*, 23-38.

Everitt, B.J., Morris, K.A., O'Brien, A., & Robbins, T.W. (1991). The basolateral amygdala-ventral striatal system and conditioned place preference: further evidence of limbic-striatal interactions underlying reward-related processes. *Neuroscience, 42*, 1-18.

Facchinetti, L.D., Imbiriba, L.A., Azevedo, T.M., Vargas, C.D., & Volchan, E. (2006). Postural modulation induced by pictures depicting prosocial or dangerous contexts. *Neuroscience Letters, 410*, 52-56.

Fehr, B., & Russell, J. A. (1984). Concept of emotion viewed from a prototype perspective. *Journal of Experimental Psychology: General, 113*, 464-486.

Fischer, S., Hallschmid, M., Elsner, A.L., & Born, J. (2002). Sleep forms memory for finger skills. *Proceedings of the National Academy of Sciences, U.S.A., 99*, 11987-11991.

Fischer, S., Drosopoulos, S., Tsen, J., & Born, J. (2006). Implicit learning-explicit knowing: A role for sleep in memory system interaction. *Journal of Cognitive Neuroscience, 18*, 311–319.

Fitts, P.M., & Posner, M.I. (1967). *Human performance.* Belmont, CA: Brooks/Cole.

French, S.J., Hailstone, J.C., & Totterdell, S. (2003). Basolateral amygdala efferents to the ventral subiculum preferentially innervate pyramidal cell dendritic spines. *Brain Research, 981*, 160-167.

Frijda, N.H. (1986). *The emotions.* Cambridge: Cambridge University Press.

Fritz, T., Jentscke, S., Gosselin, N., Sammler, D., Peretz, I., Turner, R., Friederici, A.D., & Koelsch, S. (2009). Universal recognition of three basic emotions in music. *Current Biology, 19*, 573-576.

Gabrieli, J.D.E., Stebbins, G.T., Singh, J., Willingham, D.B., & Goetz, C.G. (1997). Intact mirror-tracing and impaired rotary-pursuit skill learning in patients with Huntington's disease: Evidence for dissociable memory systems in skill learning. *Neuropsychology, 11*, 272-281.

Gray, T.S. (1999). Functional and anatomical relationships among the amygdala, basal forebrain, ventral striatum, and cortex: an integrative discussion. *Annals of the New York Academy of Sciences, 877*, 439-444.

Greene, C.M., Bahri, P., & Soto, D. (2010). Interplay between affect and arousal in recognition memory. *PLoS One, 5*, e11739.

Groenewegen, H.J., Wright, C.I., & Beijer, A.V. (1996). The nucleus accumbens: gateway for limbic structures to reach the motor system. *Progress in Brain Research, 107*, 485-511.

Groenewegen, H.J. (2003). The basal ganglia and motor control. *Neural Plasticity, 10*, 107-120.

Groenewegen, H.J., & Trimble, M. (2007). The ventral striatum as an interface between the limbic and motor systems. *CNS Spectrums, 12*, 887-892.

Goedert, K.M., & Willingham D.B. (2002). Patterns of interference in sequence learning and prism adaptation inconsistent with the consolidation hypothesis. *Learning & Memory, 9*, 279-292.

Güntürkün, O., & Kesch, S. (1987). Visual lateralization during feeding in pigeons. *Behavioral Neuroscience, 101*, 433–435.

Güntürkün, O. (1997). Avian visual lateralization: A review. *Neuroreport, 8*, 3–11.

Hajcak, G., Molnar, C., George, M.S., Bolger, K., Koola, J., & Nahas, Z. (2007). Emotion facilitates action: A transcranial magnetic stimulation study of motor cortex excitability during picture-viewing. *Psychophysiology, 44*, 91-97.

Halberstadt, J.B., & Niedenthal, P.M. (1997). Emotional state and the use of stimulus dimensions in judgment. *Journal of Personality and Social Psychology, 72*, 1017-1033.

Hazeltine, E., Grafton, S.T., & Ivry, R. (1997). Attention and stimulus characteristics determine the locus of motor-sequence encoding. A PET study. *Brain, 120*, 123-140.

Heilman, K. M., & Van Den Abell, T. (1980). Right hemisphere dominance for attention: the mechanism underlying hemispheric asymmetries of inattention (neglect). *Neurology, 30*, 327-330.

Heuer, F., & Reisberg, D. (1990). Vivid memories of emotional events: The accuracy of remembered minutiae. *Memory & Cognition, 18*, 496-506.

Hikosaka, O., Nakahara, H., Rand, M.K., Sakai, K., Lu, X., Nakamura, K., Miyachi, S., & Doya, K. (1999). Parallel neural networks for learning sequential procedures. *Trends in Neurosciences, 22*, 464-471.

Hillman, C.H., Hsiao-Wecksler, E.T., & Rosengren, K.S. (2005). Postural and eye-blink indices of the defensive startle reflex. *International Journal of Psychophysiology, 55*, 45-49.

Hirst, W., Phelps, E. A., Buckner, R. L., Budson, A. E., Cuc, A., Gabrieli, J.D., et al. (2009). Long-term memory for the terrorist attack of September 11: Flashbulb Memories, event memories, and the factors that influence their retention. *Journal of Experimental Psychology: General, 138*, 161-176.

Hoang, L.T., & Kesner, R.P. (2008). Dorsal hippocampus, CA3, and CA1 lesions disrupt temporal sequence completion. *Behavioral Neuroscience, 122*, 9-15.

Hugdahl, K., Iversen, P. M., & Johnsen, B. H. (1993). Laterality for facial expressions: does the sex of the subject interact with the sex of the stimulus face? *Cortex, 29*, 325–331.

Hull, C. L. (1943). *Principles of Behavior: An introduction to behavior theory*. New York: Appleton-Century-Crofts.

James, W. (1884). What is an emotion? *Mind, 9*, 188-205.

James, W. (1890). *The principles of psychology*. New York: H. Holt and company, online available at http://psychclassics.yorku.ca/James/Principles/.

Jansari, A., Tranel, D., & Adolphs, R. (2000). A valence-specific lateral bias for discriminating emotional facial expressions in free field. *Cognition and Emotion, 14*, 341-353.

Javadi, A.H., Walsh, V., & Lewis, P.A. (2010). Offline consolidation of procedural skill learning is enhanced by negative emotional content. *Experimental Brain Research, 208,* 507-517.

Jenkins, I.H., Brooks, D.J., Nixon, P.D., Frackowiak, R.S., & Passingham, R.E. (1994). Motor sequence learning: a study with positron emission tomography. *The Journal of Neuroscience, 14,* 3775-3790.

Johnson, L.R., Aylward, R.L., Hussain, Z., & Totterdell, S. (1994). Input from the amygdala to the rat nucleus accumbens: its relationship with tyrosine hydroxylase immunoreactivity and identified neurons. *Neuroscience, 61,* 851–865.

Jones, N. A., & Fox, N. (1992). Electroencephalogram asymmetry during emotionally evocative films and its relation to positive and negative affectivity. *Brain and Cognition, 20,* 280-299.

Judde, S., & Rickard, N. (2010). The effect of post-learning presentation of music on long-term word-list retention. *Neurobiology of Learning and Memory, 94,* 13-20.

Jueptner, M., Frith, C.D., Brooks, D.J., Frackowiak, R.S., & Passingham, R.E. (1997). Anatomy of motor learning. II. Subcortical structures and learning by trial and error. *Journal of Neurophysiology, 77,* 1325–1337.

Karni, A., Meyer, G., Rey-Hipolito, C., Jezzard, P., Adams, M.M., & Turner, R., & Ungerleider, L.G. (1998). The acquisition of skilled motor performance: fast and slow experience-driven changes in primary motor cortex. *Proceedings of the National Academy of Sciences, U.S.A., 95,* 861-868.

Keisler, A., Ashe, J., & Willingham, D.T. (2007). Time of day accounts for overnight improvement in sequence learning. *Learning & Memory, 14,* 669-672.

Keisler, A., & Shadmehr, R. (2010). Shared resource between declarative memory and motor memory. *The Journal of Neuroscience 30,* 14817–14823.

Kensinger, E.A., & Corkin, S. (2003). Memory enhancement for emotional words: Are emotional words more vividly remembered than neutral words? *Memory and Cognition, 31,* 1169-1180.

Kensinger, E. A. (2004). Remembering emotional experiences: The contribution of valence and arousal. *Reviews in the Neurosciences, 15,* 241-251.

Kensinger, E.A., & Corkin, S. (2004). Two routes to emotional memory: distinct neural processes for valence and arousal. *Proceedings of the National Academy of Sciences, U.S.A.*, 101, 3310-3315.

Kensinger, E.A., Garoff-Eaton, R.J., & Schacter, D.L. (2006). Memory for specific visual details can be enhanced by negative arousing content. *Journal of Memory and Language, 54*, 99-112.

Kensinger, E. A., Garoff-Eaton, R. J., & Schacter, D. L. (2007). Effects of emotion on memory specificity in young and older adults. *Journal of Gerontology: Psychological Sciences, 62*, 208-215.

Kensinger, E. A., & Schacter, D. L. (2008a). Neural processes supporting young and older adults' emotional memories. *Journal of Cognitive Neuroscience, 7*, 1-13.

Kensinger, E.A., & Schacter, D.L. (2008b). Memory and Emotion. In M. Lewis, J. M. Haviland-Jones and L. F. Barrett (Eds.), *The Handbook of Emotion*, 3rd Edition. New York: Guilford.

Kensinger, E. A. (2009). Remembering the Details: Effects of Emotion. *Emotion Review, 1*, 99-113.

Kensinger, E. A., & Choi, E. S. (2009). When side matters: Hemispheric processing and the visual specificity of emotional memories. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 35*, 247-253.

Kermadi, I., & Joseph, J.P. (1995). Activity in the caudate nucleus of monkey during spatial sequencing. *Journal of Neurophysiology, 74*, 911-933.

Killgore, W. D., & Yurgelun-Todd, D. A. (2007). The right-hemisphere and valence hypotheses: could they both be right (and sometimes left)? *Social Cognitive and Affective Neuroscience, 2*, 240-250.

Kimura, Y., Yoshino, A., Takahashi, Y., & Nomura, S. (2004). Interhemispheric difference in emotional response without awareness. *Psychology & Behavior, 82*, 727-731.

Knight, M., & Mather, M. (2009). Reconciling findings of emotion-induced memory enhancement and impairment of preceding items. *Emotion, 9*, 763-781.

Koch, M. (1999). The neurobiology of startle. *Progress in Neurobiology, 59*, 107-128.

Koelsch, S. (2010). Towards a neural basis of music-evoked emotions. *Trends in Cognitive Sciences, 14*, 131-137.

Kosslyn, S.M. (1987). Seeing and imagining in the cerebral hemispheres: a computational approach. *Psychological Review, 94*, 148-175.

Kosslyn, S.M., Koenig, O., Barrett, A., Cave, C.B., Tang, J., & Gabrieli, J.D. (1989). Evidence for two types of spatial representations: hemispheric specialization for categorical and coordinate relations. *Journal of Experimental Psychology: Human Perception and Performance, 15*, 723-735.

Krakauer, J.W., & Shadmehr, R. (2006). Consolidation of motor memory. *Trends in Neurosciences, 29*, 58-64.

Krumhansl, C.L. (1997). An exploratory study of musical emotions and psychophysiology. *Canadian Journal of Experimental Psychology, 51*, 336-353.

Kuchinke, L., Jacobs, A. M., Võ, M. L., Conrad, M., Grubich, C., & Herrmann, M. (2006). Modulation of prefrontal cortex activation by emotional words in recognition memory. *NeuroReport, 17*, 1037-1041.

LaBar, K.S., & Phelps, E.A. (1998). Arousal-mediated memory consolidation: role of the medial temporal lobe in humans. *Psychological Science, 9*, 490-493.

LaBar, K.S., & Cabeza, R. (2006). Cognitive neuroscience of emotional memory. Nature Reviews Neuroscience, 7, 54-64.

Laforce, R. Jr., & Doyon, J. (2001). Distinct contribution of the striatum and cerebellum to motor learning. *Brain and Cognition, 45*, 189-211.

LaLumiere, R.T., Buen, T.V., & McGaugh, J.L. (2003). Post-training intra-basolateral amygdala infusions of norepinephrine enhance consolidation of memory for contextual fear conditioning. *The Journal of Neuroscience, 23*, 6754-6758.

LaLumiere, R.T., Nguyen, L.T., & McGaugh, J.L. (2004). Post-training intrabasolateral amygdala infusions of dopamine modulate consolidation of inhibitory avoidance memory: Involvement of noradrenergic and cholinergic systems. *European Journal of Neuroscience, 20*, 2804-2810.

LaLumiere, R.T., Nawar, E.M., & McGaugh, J.L. (2005). Modulation of memory consolidation by the basolateral amygdala or nucleus accumbens shell requires concurrent dopamine receptor activation in both brain regions. *Learning & Memory, 12*, 296-301.

Lang, P. J., Bradley, M. M., & Cuthbert, B. N. (1990). Emotion, attention, and the startle reflex. *Psychological Review, 97*, 377-395.

Lang, P. J., Bradley, M. M., & Cuthbert, B. N. (1997). Motivated attention: Affect, activation, and action. In P. J. Lang, R. F. Simon, & M. T. Balaban (Eds.), *Attention and orienting: sensory and motivational processes.* Hillsdale, N.J.: Erlbaum.

Lang, P. J., Bradley, M. M., & Cuthbert, B. N. (2005). *International affective picture system (IAPS): Affective ratings of pictures and instruction manual.* Technical Report A-6. University of Florida, Gainesville, FL.

Lange, C. (1887). *Über Gemühtsbewegungen.* Leipzig: T. Thomas, online available at http://psychclassics.yorku.ca/Lange/.

Lavender, T., & Hommel, B. (2007). Affect and action: toward an event-coding account. *Emotion and Cognition, 21*, 1270-1296.

Lau, B, & Salzman, C.D. (2009). The rhythms of learning. Nature Neuroscience 12: 675-676.

Lazarus, R. S. (2000). How emotions influence performance in competitive sports. *Sport Psychologist, 14*, 229-252.

Lee, I., Jerman, T.S., & Kesner, R.P. (2005). Disruption of delayed memory for a sequence of spatial locations following CA1- or CA3-lesions of the dorsal hippocampus. *Neurobiology of Learning and Memory, 84*, 138–147.

Lehéricy, S., Benali, H., Van de Moortele, P.F., Pélégrini-Issac, M., Waechter, T., Ugurbil, K., & Doyon, J. (2005). Distinct basal ganglia territories are engaged in early and advanced motor sequence learning. *Proceedings of the National Academy of Sciences, U.S.A., 102*, 12566-12571.

Lehn, H., Steffenach, H.A., van Strien, N.M., Veltman, D.J., Witter, M.P., & Håberg, A.K. (2009). A Specific Role of the Human Hippocampus in Recall of Temporal Sequences. *The Journal of Neuroscience, 29*, 3475-3484.

Lippolis, G., Bisazza, A., Rogers, L. J., & Vallortigara, G. (2002). Lateralization of predator avoidance responses in three species of toads. *Laterality, 7*, 163-183.

Mandal, M. K., Tandon, S. C., & Asthana, H. S. (1991). Right brain damage impairs recognition of negative emotions. *Cortex, 27*, 247–253.

Marsh, A. A., Kleck, R. E., & Ambady, N. (2005). The effects of fear and anger facial expressions on approach- and avoidance-related behaviors. *Emotion, 5*, 119-124.

Mather, M., & Carstensen, L.L. (2005). Aging and motivated cognition: the positivity effect in attention and memory. *Trends in Cognitive Science, 9*, 496-502.

Maxwell, J. S., & Davidson, R. J. (2007). Emotion as motion: Asymmetries in approach and avoidant actions. *Psychological Science, 18*, 1113-1119.

McDonald, A.J. (1991) Topographical organization of amygdaloid projections to the caudatoputamen, nucleus accumbens, and related striatal-like areas of the rat brain. *Neuroscience,* 44, 15-33.

McGaugh, J.L. (2004). The amygdala modulates the consolidation of memories of emotionally arousing experiences. *Annual Review of Neuroscience, 27*, 1-28.

McGeer, P.L., McGeer, E.G., Scherer, U., & Singh, K. (1977). A glutamatergic corticostriatal path? *Brain Research, 128*, 369-373.

McLaren, J., & Bryson, S. E. (1987). Hemispheric asymmetries in the perception of emotional and neutral faces. *Cortex, 23*, 645-654.

Miranda, M.I., LaLumiere, R.T., Buen, T.V., Bermudez-Rattoni, F., & McGaugh, J.L. (2003). Blockade of noradrenergic receptors in the basolateral amygdala impairs taste memory. *European Journal of Neuroscience, 18*, 2605-2610.

Miyachi, S., Hikosaka, O., Miyashita, K., Karadi, Z., & Rand, M.K. (1997). Differential roles of monkey striatum in learning of sequential hand movement. *Experimental Brain Research, 115*, 1-5.

Miyachi, S., Hikosaka, O., & Lu, X. (2002). Differential activation of monkey striatal neurons in the early and late stages of procedural learning. *Experimental Brain Research, 146*, 122-126.

Moreno, C. R., Borod, J. C., Welkowitz, J., & Alpert, M. (1990). Lateralization for the expression and perception of facial emotion as a function of age. *Neuropsychologia, 28*, 199-209.

Muellbacher, W., Ziemann, U., Wissel, J., Dang, N., Kofler, M., Facchini, S., Boroojerdi, B., Poewe, W., & Hallen, M. (2002). Early consolidation in human primary motor kortex. *Nature, 7*, 640-644.

Murphy, F. C., Nimmo-Smith, I., & Lawrence, A. D. (2003). Functional neuroanatomy of emotions: A meta-analysis. *Cognitive, Affective, & Behavioral Neuroscience, 3*, 207-233.

Nakamura, T., Ghilardi, M.F., Mentis, M., Dhawan, V., Fukuda, M., Hacking, A., Moeller, J.R., Ghez, C., & Eidelberg, D. (2001). Functional networks in motor sequence learning: abnormal topographies in Parkinson's disease. *Human Brain Mapping, 12*, 42-60.

Narumoto, J., Okada, T., Sadato, N., Fukui, K., & Yonekura, Y. (2001). Attention to emotion modulates fMRI activity in human right superior temporal sulcus. *Cognitive Brain Research, 12*, 225-241.

Natale, M., Gur, R. E., & Gur, R. C. (1983). Hemispheric asymmetries in processing emotional expressions. *Neuropsychologia, 21*, 555-565.

Nemeth, D., Janacsek, K., Londe, Z., Ullman, M.T., Howard, D.V., & Howard, J.H. (2010). Sleep has no critical role in implicit motor sequence learning in young and old adults. *Experimental Brain Research, 201*, 351-358.

Nielson, K.A., & Bryant, T. (2005). The effects of non-contingent extrinsic and intrinsic rewards on memory consolidation. *Neurobiology of Learning and Memory, 84*, 42-48.

Nielson, K.A., & Powless, M. (2007). Positive and negative sources of emotional arousal enhance long-term word-list retention when induced as long as 30 min after learning. *Neurobiology of Learning and Memory, 88*, 40-47.

Nishida, M., & Walker, M.P. (2007). Daytime naps, motor memory consolidation and regionally specific sleep spindles. *PLoS One, 2*, e341.

Nissen, M.J., & Bullemer, P. (1987). Attentional requirements of learning: evidence from performance measures. *Cognitive Psychology, 19*, 1-32.

Noesselt, T., Driver, J., Heinze, H. J., & Dolan, R. (2005). Asymmetrical activation in the human brain during processing of fearful faces. *Current Biology, 15*, 424-429.

Ochsner, K.N. (2000). Are affective events richly "remembered" or simply familiar? The experience and process of recognizing feelings past. *Journal of Experimental Psychology: General, 129*, 242-261.

Oldfield, R. C. (1971). The assessment and the analysis of handedness: the Edinburgh inventory. *Neuropsychologia, 9*, 97-113.

Osgood, C.E., Suci, G.J., & Tannenbaum, P.H. (1957). *The Measurement of Meaning*. Urbana: IL. University of Illinois Press.

Pauli, P., Wiedemann, G., & Nickola, M. (1999). Pain sensitivity, cerebral laterality, and negative affect. *Pain, 80*, 359-364.

Paz, R., Gelbard-Sagiv, H., Mukamel, R., Harel, M., Malach, R., & Fried, I. (2010). A neural substrate in the human hippocampus for linking successive events. *Proceedings of the National Academy of Sciences, U.S.A., 107*, 6046-6051.

Peretz, I., Gagnon, L., & Bouchard, B. (1998). Music and emotion: perceptual determinants, immediacy, and isolation after brain damage. *Cognition, 68,* 111-141.

Pezze, M.A., Feldon, J., & Murphy, C.A. (2002). Increased conditioned fear response and altered balance of dopamine in the shell and core of the nucleus accumbens during amphetamine withdrawal. *Neuropharmacology, 42,* 633-643.

Phelps, E.A. (2004). Human emotion and memory: Interactions of the amygdala and hippocampal complex. *Current Opinion in Neurobiology, 14,* 198-202.

Poldrack, R.A., Sabb, F.W., Foerde, K., Tom, S.M, Asarnow, R.F, Bookheimer, S.Y., & Knowlton, B.J. (2005). The neural correlates of motor skill automaticity. *The Journal of Neuroscience, 25,* 5356-5364.

Proctor, R.W., & Dutta, A. (1995). *Skill acquisition and human performance.* Thousand Oaks, CA: Sage Publications.

Rauch, S. L., van der Kolk, B. A., Fisler, R. E., Alpert, N. M., Orr, S. P., Savage, C. R., Fischman, A.J., Jenike, M.A., & Pitman, R.K. (1996). A symptom provocation study of posttraumatic stress disorder using positron emission tomography and script-driven imagery. *Archives of General Psychiatry, 53,* 380-387.

Reis, J., Schambra, H.M., Cohen, L.G., Buch, E.R., Fritsch, B., Zarahn, E., Celnik, P.A., & Krakauer, J.W. (2009). Noninvasive cortical stimulation enhances motor skill acquisition over multiple days through an effect on consolidation. *Proceedings of the National Academy of Sciences, U.S.A., 106,* 1590-1595.

Reuter-Lorenz, P., & Davidson, R. J. (1981). Differential contributions of the two cerebral hemispheres to the perception of happy and sad faces. *Neuropsychologia, 19,* 609-613.

Rinck, M., & Becker, E. S. (2007). Approach and avoidance in fear of spiders. *Journal of Behavior Therapy and Experimental Psychiatry, 38,* 105-120.

Robertson, E.M., Pascual-Leone, A., & Miall, R.C. (2004) Current concepts in procedural consolidation. *Nature Reviews Neuroscience, 5,* 576-582.

Robertson, E.M., Pascual-Leone, A., & Press, D.Z. (2004). Awareness modifies the skill-learning benefits of sleep. *Current Biology, 14,* 208-212.

Robertson, E.M. (2007). The serial reaction time task: implicit motor skill learning? *The Journal of Neuroscience, 27,* 10073-10075.

Robins, A., & Rogers, L. J. (2004). Lateralized prey-catching responses in the cane toad, Bufo marinus: analysis of complex visual stimuli. *Animal Behaviour, 68,* 767-775.

Rodway, P., & Schepman, A. (2007). Valence specific laterality effects in prosody: expectancy account and the effects of morphed prosody and stimulus lead. *Brain and Cognition, 63,* 31-41.

Roozendaal, B., de Quervain, D.J., Ferry, B., Setlow, B., & McGaugh, J.L. (2001). Basolateral amygdala-nucleus accumbens interactions in mediating glucocorticoid enhancement of memory consolidation. *The Journal of Neuroscience, 21,* 2518-2525.

Roozendaal, B., Hui, G.K., Hui, I.R., Berlau, D.J, McGaugh, J.L., & Weinberger, N.M. (2006). Basolateral amygdala noradrenergic activity mediates corticosterone-induced enhancement of auditory fear conditioning. *Neurobiology of Learning and Memory, 86,* 249-255.

Rotteveel, M., & Phaf, R. H. (2004). Automatic affective evaluation does not automatically predispose for arm flexion and extension. *Emotion, 4,* 156-172.

Rubin, D.C., & Kozin, M. (1984). Vivid memories. *Cognition, 16,* 63-80.

Russell, J. A., & Barrett, L. F. (1999). Core affect, prototypical emotional episodes, and other things called emotion: Dissecting the elephant. *Journal of Personality and Social Psychology, 76,* 805-819.

Sah, P., Faber, E.S., Lopez De Armentia, M., & Power, J. (2003). The Amygdaloid Complex: Anatomy and Physiology. *Physiological Reviews, 83,* 803-834.

Sato, W., Kochiyama, T., Yoshikawa, S., Naito, E., & Matsumura, M. (2004). Enhanced neural activity in response to dynamic facial expressions of emotion: An fMRI study. *Cognitive Brain Research, 20,* 81-91.

Sato, W., & Aoki, S. (2006). Right hemispheric dominance in processing of unconscious negative emotion**.** *Brain and Cognition, 62,* 261-266.

Schacter, D. L. (1987). Implicit memory: History and Current status. *Journal of Experimental Psychology: Learning, Memory and Cognition, 13,* 501-518.

Scherer, K.R. (2000). Psychological models of emotion. In J. Borod (Ed.), *The neuropsychology of emotion (*pp.137-162). Oxford/New York: Oxford University Press.

Scherer, K. R. (2001). Appraisal considered as a process of multi-level sequential checking. In K. R. Scherer, A. Schorr, & T. Johnstone (Eds.), *Appraisal processes in emotion: Theory, methods, research* (pp. 92-120). New York and Oxford: Oxford University Press.

Schiff, B. B., & Bassel, C. (1996). Effects of asymmetrical hemispheric activation on approach and withdrawal responses. *Neuropsychology, 10*, 557-564.

Schmidt, R.A. (1988). *Motor Control and Learning: A Behavioral Emphasis*. 2nd ed. Champaign, IL: Human Kinetics.

Setlow, B., Roozendaal, B., & McGaugh, J.L. (2000). Involvement of a basolateral amygdala complex-nucleus accumbens pathway in glucocorticoid-induced modulation of memory consolidation. *European Journal of Neuroscience, 12*, 367-375.

Shadmehr, R, & Brashers-Krug, T. (1997). Functional stages in the formation of human long-term motor memory. *The Journal of Neuroscience, 17*, 409-419.

Silberman, E. K, & Weingartner, H. (1986). Hemispheric lateralization of functions related to emotion. *Brain and Cognition, 5*, 322-353.

Simon-Thomas, E. R., Role, K. O., & Knight, R. T. (2005). Behavioral and electrophysiological evidence of a right hemisphere bias for the influence of negative emotion on higher cognition. *Journal of Cognitive Neuroscience, 17*, 518-529.

Small, D.M., Gregory, M.D., Mak, Y.E., Gitelman, D., Mesulam, M.M., & Parrish, T. (2003). Dissociation of neural representation of intensity and affective valuation in human gustation. *Neuron, 39*, 701-711.

Smith, C.N., Hopkins, R.O., & Squire, L.R. (2006). Experience-dependent eye movements, awareness, and hippocampus-dependent memory. *The Journal of Neuroscience, 26*, 11304-11312.

Smith, S. D., & Bulman-Fleming, M. B. (2004). A hemispheric asymmetry for the unconscious perception of emotion. *Brain and Cognition, 55*, 452-457.

Sobotka, S. S., Davidson, R. J., & Senulis, J. A. (1992). Anterior brain electrical asymmetries in response to reward and punishment. *Electroencephalography and Clinical Neurophysiology, 83*, 236-247.

Solarz, A. K. (1960). Latency of instrumental responses as a function of compatibility with the meaning of eliciting verbal signs. *Journal of Experimental Psychology, 59*, 239-245.

Song, S., Howard, J.H., Jr., & Howard, D.V. (2007). Sleep does not benefit probabilistic motor sequence learning. *The Journal of Neuroscience, 27*, 12475-12483.

Spielberger, C.D., & Diaz-Guerrero, R. (1983). Cross-cultural anxiety. *Series in Clinical & Community Psychology: Stress & Anxiety, 2*, 218.

Stefan, K., Wycislo, M., Gentner, R., Schramm, A., Naumann, M., Reiners, K., & Classen, J. (2006). Temporary occlusion of associative motor cortical plasticity by prior dynamic motor training. *Cerebral Cortex, 16*, 376-385.

Squire, L. R. (1992). Memory and the hippocampus: A synthesis from findings with rats, monkeys, and humans. *Psychological Review, 99*, 195-231.

Squire L. R., & Zola S. M. (1996). Structure and function of declarative and nondeclarative memory systems. *Proceedings of the National Academy of Sciences, U.S.A., 93*, 13515-13522.

Tamietto, M., Latini Corazzini, L., de Gelder, B., & Geminiani, G. (2006). Functional asymmetry and interhemispheric cooperation in the perception of emotions from facial expressions. *Experimental Brain Research, 171*, 389-404.

Talmi, D., & Moscovitch, M. (2004). Can semantic relatedness explain the enhancement of memory for emotional words? *Memory and Cognition, 32*, 742-751.

Terry, P. C. (2004). Mood and emotions in sport. In T. Morris & J. Summers (Eds.), *Sport psychology: Theory, applications and issues* (2nd ed., pp. 48-73). John Wiley & Sons Australia.

Valenti, A., Sovrano, V. A., Zucca, P., & Vallortigara, G. (2003). Visual lateralization in quails. *Laterality, 8*, 67-78.

Vallortigara, G., Regolin, L., Bortolomiol, G., & Tommasi, L. (1996). Lateral asymmetries due to preferences in eye use during visual discrimination learning in chicks. *Behavioural Brain Research, 74*, 135-143.

Van Dantzig, S., Pecher, D., & Zwaan, R. A. (2008). Approach and avoidance as action effects. *Quarterly Journal of Experimental Psychology, 61*, 1298-1306.

Ventolini, N., Ferrero, E., Sponza, S., Della Chiesa, A., Zucca, P., & Vallortigara, G. (2005). Laterality in the wild: Preferential hemifield use during predatory and sexual behaviour in the black winged stilt (Himantopus himantopus). *Animal Behaviour, 69*, 1077-1084.

Vrana, S.R., & Lang, P.J. (1990). Fear imagery and the startle probe reflex. *Journal of Abnormal Psychology, 99*, 189-197.

Walker, M.P., Brakefield, T., Morgan, A., Hobson, J.A., & Stickgold, R. (2002). Practice with sleep makes perfect: sleep-dependent motor skill learning. *Neuron, 35*, 205-211.

Walker, M.P., Brakefield, T., Hobson, J.A., & Stickgold, R. (2003). Dissociable stages of human memory consolidation and reconsolidation. *Nature, 425*, 616-620.

Walker, M.P., & Stickgold, R. (2004). Sleep-dependent learning and memory consolidation. *Neuron, 44*, 121-133.

Walker, M.P. (2005). A refined model of sleep and the time course of memory formation. *Behavioral and Brain Sciences, 28*, 51-64.

Watson, D., Clark, L.A., & Tellegen, A. (1988). Development and validation of brief measures of positive and negative affect: The PANAS scales. *Journal of Personality and Social Psychology, 54*, 1063-1070.

Wentura, D., Rothermund, K., & Bak, P. (2000). Automatic vigilance: the attention-grabbing power of approach- and avoidance-related social information. *Journal of Personality and Social Psychology, 78*, 1024-1037.

White, R.T. (2002). Memory for events after twenty years. *Applied Cognitive Psychology, 16*, 603-612.

Wiedemann, G., Pauli, P., Dengler, W., Lutzenberger, W., Birbaumer, N., & Buchkremer, G. (1999). Frontal brain asymmetry as a biological substrate of emotions in patients with panic disorders. *Archives of General Psychiatry, 56*, 78-84.

Willingham, D.B., Nissen, M.J., & Bullemer, P. (1989). On the development of procedural knowledge. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 15*, 1047-1060.

Willingham, D.B., & Dumas, J.A. (1997). Long term retention of a motor skill: Implicit sequence knowledge is not retained after a one year delay. *Psychological Research, 60*, 113-119.

Willingham, D.B., Salidis, J., & Gabrieli, J.D.E. (2002). Direct comparison of neural systems mediating conscious and unconscious skill learning. *Journal of Neurophysiology, 88*, 1451-1460.

Wright, C.I., Beijer, A.V., & Groenewegen, H.J. (1996). Basal amygdaloid complex afferents to the rat nucleus accumbens are compartmentally organized. *The Journal of Neuroscience, 16,* 1877-1893.

Wulf, G. (2007). *Attention and motor skill learning*. Champaign, IL: Human Kinetics.

Yerkes, R. M., & Dodson, J. D. (1908). The relationship of strength of stimulus to rapidity of habit formation. *Journal of Comparative and Neurological Psychology, 18,* 459-482.

Yin, H.H. (2010). The sensorimotor striatum is necessary for serial order learning. *The Journal of Neuroscience, 30,* 14719-14723.

Appendix

Materials: Experiment 1

Probandeninformation

Wissenschaftliche neuropsychologische Untersuchungen zum Gedächtnis für Bewegungen

Liebe Probandin, lieber Proband,

wir laden Sie ein, an einer neuropsychologischen Untersuchung an der Neurologischen Klinik der Universität Würzburg teilzunehmen. Es ist wichtig, dass Sie zunächst verschiedene allgemeine Prinzipien verstehen, die auf alle Personen anzuwenden sind, die an unseren Untersuchungen beteiligt sind: (a) die Teilnahme ist vollständig freiwillig; (b) Sie selbst gewinnen keinen persönlichen Nutzen aus der Untersuchung; (c) Sie können aus der Untersuchung jederzeit ausscheiden, ohne dass Sie deshalb befürchten müssen, einen Nachteil zu erleiden. Wir bitten Sie, alle Fragen, die Sie noch haben, mit den die Untersuchung durchführenden Ärzten oder Psychologen zu besprechen.
Das Ziel unserer Untersuchung ist es, die Mechanismen zu erforschen, die das Gehirn befähigen, Bewegungen zu lernen.

Welche Techniken werden verwendet?
Sie werden eine motorische Lernaufgabe üben. Dabei müssen Sie schnelle, seitliche Bewegungen mit ihrem rechten Daumen ausführen. Die Kraft, die Sie dabei einsetzen, wird von einem Kraftaufnehmer aufgezeichnet und das Kraftsignal wird für Sie auf einem Bildschirm dargestellt.

Wie laufen die Untersuchungen ab?
Am Anfang werden Sie die Aufgabe trainieren, bis Ihnen der Ablauf klar ist. Die Aufgabe besteht aus 5 Experimentblöcken. Jeder Block dauert etwa 3.5 min. Im 2., 3. und 4. Block werden Sie mit einem Kopfhörer verschiedene Geräusche hören. Zwischen den Blöcken können Sie etwa 1 min. Pause machen. Insgesamt werden Sie für die Aufgabe etwa 20 min benötigen.
Die Daumenbewegung wird jeweils auf ein optisches Signal hin ausgeführt. Pro Block sollen 100 Daumenbewegungen gemacht werden. Dabei sollen Sie lernen, Ihre Kraft so einzusetzen, dass die Anzeige auf dem Bildschirm so oft wie möglich innerhalb des dort vorgegebenen Korridors bleibt.

Mit welchen Risiken oder Nebenwirkungen muss ich rechnen?
Es gibt keine bekannten Nebenwirkungen.

Materials: Experiment 2

Probandeninformation

Wissenschaftliche neuropsychologische Untersuchung

zum Gedächtnis für Bewegungen

Liebe Probandin, lieber Proband,

wir laden Sie ein, an einer neuropsychologischen Untersuchung an der Neurologischen Klinik der Universität Würzburg teilzunehmen. Es ist wichtig, dass Sie zunächst verschiedene allgemeine Prinzipien verstehen, die auf alle Personen anzuwenden sind, die an unseren Untersuchungen beteiligt sind: (a) die Teilnahme ist vollständig freiwillig; (b) Sie selbst gewinnen keinen persönlichen Nutzen aus der Untersuchung; (c) Sie können aus der Untersuchung jederzeit ausscheiden, ohne dass Sie deshalb befürchten müssen, einen Nachteil zu erleiden.

Wir bitten Sie, alle Fragen, die Sie haben, mit den die Untersuchung durchführenden Ärzten oder Psychologen zu besprechen.

Das Ziel unserer Untersuchung ist, das motorische Verhalten zu erforschen.

Welche Techniken werden verwendet?

Sie werden eine einfache motorische Aufgabe üben. Dabei werden Sie auf dem Bildschirm einen blauen Kreis sehen, und die Taste drücken, die der jeweiligen Position des Kreises entspricht. Vor und nach der motorischen Aufgabe werden Ihnen Bilder gezeigt, dabei werden Sie über einen Kopfhörer Musik oder ein Geräusch hören.

Mit welchen Risiken oder Nebenwirkungen muss ich rechnen?

Es gibt keine bekannten Nebenwirkungen.

Materials: Experiment 1 & 2

Einverständniserklärung

zur Durchführung einer neuropsychologischen Untersuchung

Ich habe die obige Erklärung zur Untersuchung über das motorische Verhalten gelesen und verstanden.
Ich hatte Gelegenheit, zu der Untersuchung Fragen zu stellen. Ich erkläre mich hiermit mit der Durchführung der Untersuchung einverstanden.

Datum Unterschrift der Probandin / des Probanden

Erklärung:

Mir ist bekannt, dass die im Zusammenhang mit dieser Untersuchung erhobenen Daten anonymisiert weiter verarbeitet, im Rahmen von Forschungsvorhaben anonymisiert an Dritte weitergegeben werden und in der Klinik für Neurologie archiviert werden. Die geltenden Datenschutzbestimmungen werden beachtet. Ich erkläre mich mit der Veröffentlichung der im Verlauf der Untersuchung erhobenen Daten in *anonymisierter* Form einverstanden.

Mir ist weiterhin bekannt, dass die Teilnahme an der Untersuchung vollständig freiwillig ist, dass ich selbst keinen persönlichen Nutzen aus der Untersuchung gewinne und dass ich aus der Untersuchung jederzeit ausscheiden kann, ohne dass ich deshalb einen Nachteil erleide.

Datum Unterschrift Proband(in) Unterschrift des Untersuchers

Materials: Experiment 3

Probandeninformation

Wissenschaftliche psychologische Untersuchung zur Emotion

Lieber Proband, liebe Probandin

wir laden Sie ein, an einer wissenschaftlichen Untersuchung an der Biopsychologischen Abteilung der Universität Bochum teilzunehmen. Es ist wichtig, dass Sie zunächst verschiedene allgemeine Prinzipien verstehen, die auf alle Personen anzuwenden sind, die an unseren Untersuchungen beteiligt sind: (a) die Teilnahme ist vollständig freiwillig; (b) Sie selbst gewinnen keinen persönlichen Nutzen aus der Untersuchung; (c) Sie können aus der Untersuchung jederzeit ausscheiden, ohne dass Sie deshalb befürchten müssen, einen Nachteil zu erleiden.

Das Ziel der Untersuchung ist es zunächst zu erforschen, welche Beziehungen es zwischen Emotionen und Motorischem Verhalten gibt. In diesem Experiment werden Sie eine motorische Aufgabe üben, während Sie emotionale Bilder sehen.

Beispiele für Emotionale Bilder:

Positive:

Negative:

Materials: Experiment 3

Die motorische Aufgabe:

----Wenn Sie ein positives Bild sehen, sollen Sie den Joystick nach vorne schieben, und dann sollen Sie wieder zur Anfangsposition kommen.

----Wenn Sie ein negatives Bild sehen, sollen Sie den Joystick zu sich ziehen und dann sollen Sie den Joystick wieder zur Anfangsposition schieben.

Am Anfang werden Sie die Aufgabe trainieren, bis es Ihnen klar ist, wie es läuft. Der Versuchsleiter wird Ihnen am Anfang des Experiments mitteilen, mit welcher Hand Sie beginnen werden! Nach der Hälfte der Durchgänge werden Sie die Reaktionshand wechseln, daran werden wir Sie erinnern, wenn die Hälfte der Durchgänge fertig ist.

Materials: Experiment 3

Einverständniserklärung zur Teilnahme an Experimenten

Im Rahmen der biopsychologischen Forschung an der Psychologischen Fakultät der Ruhr-Universität Bochum erheben wir Daten und registrieren Ihre Reaktionen. Die erhobenen Daten werden anonymisiert gespeichert und dienen ausschließlich zu Forschungszwecken.

Wir behandeln alle Ihre Angaben vertraulich.

Ich bin darüber aufgeklärt worden, dass sämtliche persönlichen Informationen anonymisiert erhoben werden, und dass die Versuchsleiter alles ihnen mögliche tun werden, um die Vertraulichkeit zu wahren.

Hiermit erkläre ich mich mit der Teilnahme an der Untersuchung einverstanden. Ich bin über die angewandte Methode und deren Unschädlichkeit aufgeklärt worden und habe sie verstanden. Ich bin darüber informiert, dass ich jederzeit, ohne Angabe von Gründen und ohne Nachteile befürchten zu müssen, das Experiment auch vorzeitig beenden kann.

Name des Probanden: _____

Bochum, den _____ _____
Unterschrift des Probanden Unterschrift des Untersuchers

Aufnahme in die Versuchspersonendatenbank

Ich bin damit einverstanden, dass meine Email-Adresse getrennt von meinen Daten gespeichert wird und ich unter Umständen in Zukunft unverbindliche Anfragen zur Teilnahme an weiteren Studien in der Biopsychologie erhalte.

E-Mail-Adresse: _____
Geschlecht: _____
Alter: _____
Händigkeit: _____