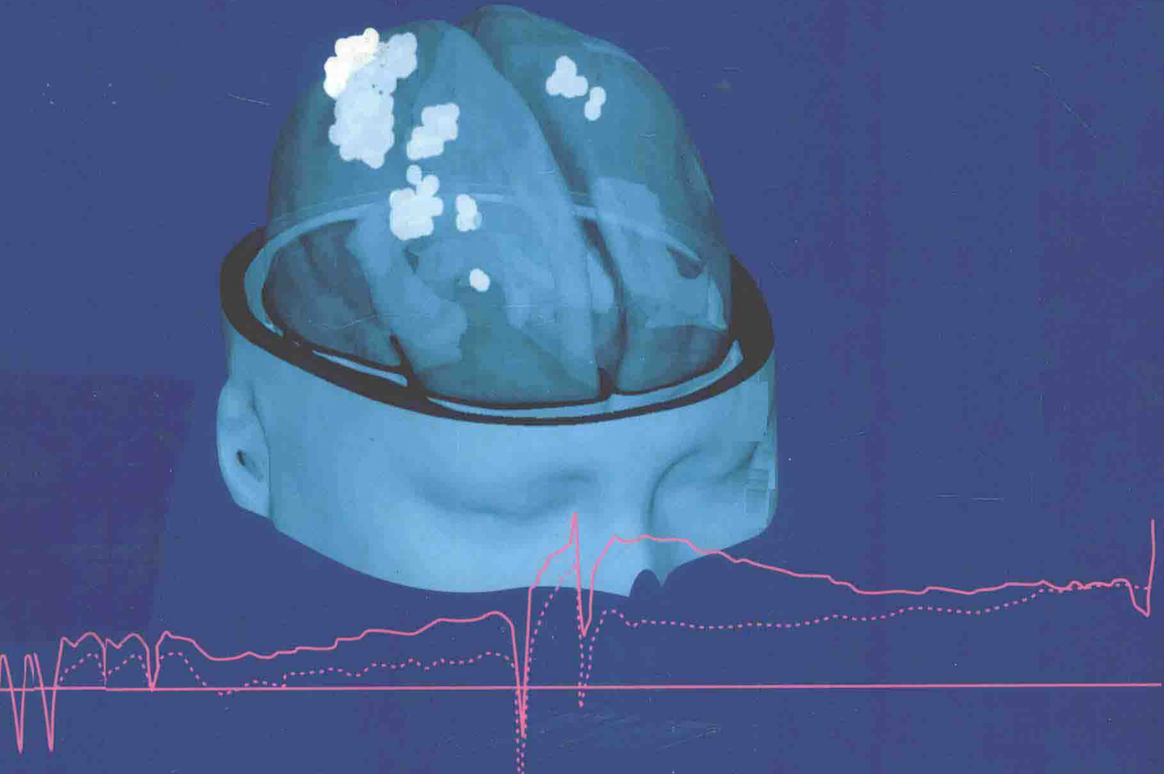
Principles of Learning and Memory

Rainer H. Kluwe
Gerd Lüer
Frank Rösler
Editors



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Preface

"How the brain enables the mind is the question to be answered in the twenty-first century…" (Gazzaniga, 1998, p. xii). This question is at the core of research on human learning and memory. Whereas previous attempts at addressing Gazzaniga's "grand question" have focused solely on psychological processes, researchers are now calling for interdisciplinary work that bridges the areas cognitive psychology, cognitive neuroscience, cognitive neuropsychology, neuroanatomy, physiology and biology. This volume reviews the recent research on human learning and memory. Our goal is to provide an overview of the exciting incites provided by research investigations that meld multiple research methodologies and domains.

Research on learning and memory is performed at different levels of analysis ranging from the cell to observable behavior. The breadth of research methodologies raises the challenge of integrating the different approaches. In order to answer questions about the brain structures and systems that enable human cognitive activity, it is necessary to relate approaches and results from experimental psychology to those provided by biology, neuroanatomy, or neuroscience. The former are concerned with the systems level of behavior, the latter with more elementary levels of neurons and neuronal networks. It is only through a synthesis of the disciplines that cover the whole hierarchy of analysis, that researchers can develop a better understanding of the system, its components, its constituting elements, and, last but not least, its interaction with the environment

The emphasis of the chapters in this volume is on the interconnections between the level of behavior and the level of neural activities and structures. The goal is to overcome the traditional borders separating different fields of research in order to present an integrated pattern of results that enables a broader, interdisciplinary view and a deeper understanding of human learning and memory. The volume thus presents an interdisciplinary synthesis of current research connecting cognitive science and neuroscience.

The large amount of research and the broad range of phenomena require us to focus on selected topics. We selected phenomena that are central to human learning and memory, and that are studied from different perspectives in cognitive psychology, in neuroscience, and in biology. By analyzing the literature fifteen principles were delineated which seem to be most central for research on learning and memory and which are currently being investigated through an interdisciplinary approach. These principles can be subsumed under five main themes: (A) Formation of memories; (B) Organization of memories during encoding, storage and retrieval; (C) Consolidation of memories; (D) Control of memories during information processing; and (E) Adaptive specialization of memories.

A. Formation of memories: The human cognitive system is able to learn and to change, to improve and to adapt performance based on experience and changes in the environment. How does the brain enable learning and memory? The first four chapters by *Lachnit,* by *Kress and Daum,* by *Röder and Rösler,* and by *Roth* focus on the mechanisms and underlying brain structures that participate in the formation of new memories, i.e. on the processes that lead to the acquisition of knowledge. The chapters discuss results from animal and human research that point to four basic principles: spatio-temporal contiguity, multiple brain structures underlying experience-related changes, brain plasticity, and emotional learning.

B. Organization of memories: How are processes of encoding, storage and retrieval related to brain structures and neural processes? Probably one of the most important insights gained through recent research is that these processes are based on highly organized and specialized structures of the brain (e.g., Damasio, 1989; Squire, Knowlton, & Musen, 1993). Functional modularity of the brain is now one of the key concepts of neuroscience. Data obtained from experimental analyses of human cognitive performance as well as a theoretical analysis of memory phenomena suggest that specialized subsystems perform specific tasks like encoding, storage, retrieval, and modification of information. These systems are defined by structural and functional criteria, in particular by the type of information representation that is available to them. The goal of research is to identify such specialized subsystems and to understand their functional intricacies. This is the central issue addressed by *Rösler and Heil*, by *Buchner and Brandt,* and by *Jonides, Sylvester, Lacey, Wager, Nichols and Awh.* These chapters cover the principles of coding specific storage and retrieval, of multiple memory systems, and of separate systems of working memory.

C. Consolidation of memories: The flexible acquisition of new information is essential for systems that have to interact with a changing world. Equally important is the ability of the system to transform this new information into stable memories that can reliably guide behavior later. Chapters by *Schwarting*, by *Paller*, and by *Brand and Markowitsch* focus on the mechanisms and processes that support the consolidation of newly acquired knowledge and provide for enduring memories. These authors cover the principle of memory consolidation and its pharmacological modulation, the principle of cross-cortical consolidation of episodic memories, and the principle of bottleneck structures necessary for consolidation and retrieval.

D. Control of memories: The chapters in this section all deal with the basic mechanisms of how information is represented and how information transfer is controlled in the nervous system. The chapter of *Munk* discusses the principle of transient binding in the CNS, which is a powerful, empirically based hypothesis that explains how the brain can find its equilibrium between two seemingly antagonistic processing modes: cortical adaptivity versus consolidation, or rapid reorganization versus the generation of stabilized representations. The principle of inhibition is another basic mechanism, which regulates activation processes on both the neuronal and behavioral levels of memory representations. *Dagenbach & Kubat-Silman* review several inhibitory mechanisms, derived from cognitive psychology, that are relevant to working memory and long-term memory control. They relate these mechanisms to possible neural correlates. *Mayr's* chapter draws on recent evidence from behavioral, brain imaging, and single-cell recording work to sketch out an integrated view of the neurocognitive basis of executive control.

E. Adaptive specialization of memories: Pinker (1997), referring to Darwin's claim that future psychological research will be performed on new foundations, stated that the process of relating psychological and biological research has been slow except for the important development of evolutionary psychology, as initiated by Cosmides and colleagues (e.g. Barkow, Cosmides, & Tooby, 1992). Evolutionary psychology has engendered an unusually strong combination of approaches that includes cognitive psychology's analysis of information processing and evolutionary biology's analysis of complex, adaptive behavior of species. *Güntürkün and Durstewitz* and of *Gallistel* continue this fruitful collaboration in their chapters, which cover the principle of species independent learning phenomena and the principle of adaptive specialization.

The fifteen chapters of this volume are based on the International Symposium on Human Learning and Memory held in March 7-10, 2001. Speakers from the USA and Germany contributed to the conference and agreed also to write chapters for this textbook. These scientists, leaders in their fields, were asked to discuss principles from an interdisciplinary point of view. Due to the scope of the chapters, the volume is intended as an advanced textbook for students of the disciplines of neuroscience and cognitive science.

The editors acknowledge the financial support provided by the German Research Society (DFG, Bonn) and the State of Lower Saxony (Hannover), which supported the international conference held at the Hanse Institute for Advanced Study (Delmenhorst). The hospitality of the Hanse Institute is gratefully acknowledged. We are especially grateful for the generous support of the Academy of Sciences, Göttingen, who made this volume possible. We thank the speakers and the other participating young and senior scientists for joining the conference and for shaping the project by their lively discussions, and we thank the authors for their readiness to contribute to the volume. Special thanks go to Gale Pearce (Eugene, Oregon, USA) for examining chapters written by German authors as a native speaker, and finally to Adjuta Bertsch and Renate Kalk (Marburg, Germany) for accomplishing most of the work that was necessary to prepare a camera ready manuscript.

Hamburg, Göttingen, Marburg, September 2002

Rainer H. Kluwe
Gerd Lüer
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Section A

FORMATION OF MEMORIES

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The Principle of Contiguity

Harald Lachnit

The Law of Contiguity is considered a keystone of most scientific theories of learning, memory, and knowledge. In general, the Law of Contiguity states that after events occur together (in spatio-temporal proximity), the reoccurrence of only one event evokes the 'memory' of the others.

The present chapter is an attempt to outline how this principle stimulated theorizing as well as empirical research in the area of learning and memory, with special emphasis on the former. In part, I will follow the course of arguments put forth in the excellent review of "Classical conditioning and the Law of Contiguity" by Gormezano & Kehoe (1981).

We will start with a brief look at the historical antecedents in philosophy and early psychology from Aristotle, across British Empiricism and reflexology to behaviorism, culminating in the most unconstrained contiguity theory proposed by Guthrie (1935). From its zenith we will accompany the Principle of Contiguity while it is riding a roller coaster through a landscape of empirical attacks and theoretical rescue operations back to the significance of contiguity for learning (but not behavior). We will close with a recent attempt to renounce contiguity in favor of time and rate.

Historical Antecedents: Philosophical Roots and Early Psychology

The roots of the Law of Contiguity can be traced back to Greek philosophy. Aristotle is generally credited with originating the concepts of association and contiguity. In his discussion of memory, he stated that knowledge and mind are built from basic *sensations* which themselves are hooked together through associations. Similarity, contrast, and previous spatial or temporal contiguity of events determine which events will be recalled together.

The British Empiricists (about 1650 – 1850) were the actual predecessors to psychological theories of association. Thomas Hobbes, John Locke, Thomas Hartley, James Mill, and John Stuart Mill were opposed to the Cartesian tenet of innate ideas. Instead, they favored the idea that humans are born with a mind that is a blank slate (tabula rasa) and that all information enters the mind via simple sensory perception. These philosophers proposed the existence of a connective force – association – that enabled complex mental entities composed of simple (sensory) events. They outlined one primary and some secondary laws of association. The primary law of association was the Law of Contiguity: An association between two events will be formed only if they occur in spatio-temporal proximity. The most important secondary law of association, the Law of Frequency, states that the number of repetitions of contiguous pairings determines their subsequent associative strength. By assuming physiological vibrations as counterparts of mental events, Hartley opened a window for the evaluation of this philosophical principle by empirical sciences. Furthermore, he laid the foundation of the concept of the stimulus trace, which became very important in later days.

The crucial step in the conversion of the Law of Contiguity into a fundamental principle of learning and memory took place in the dawn of the 20th century, when Pavlov worked on the method of the conditioned reflex as a tool for the physiological study of the neural mechanisms by which animals adjust to their environments. It was Bekhterev (1913), however, who first asserted the parallels of the conditioned reflex and the associative doctrine. Lashley (1916) stated that the conditioned reflex method enables the investigator to precisely control stimuli and measure responding. Thus, Pavlovian conditioning may be considered an almost ideal example of associative learning. At about the same time, Thorndike (1913) studied animal intelligence. In his Law of Effect he stated that the connection between situation and response is strengthened when the response is closely followed by satisfaction. Hence, Thorndike's Law of Effect is a principle of association through contiguity, too. In the rise of Behaviorism, the conditioned reflex (now called conditioned response) changed from an example of association through contiguity to the substitute for the Law of Contiguity (Guthrie, 1930). Ultimately, Guthrie (1935) assumed that nothing but contiguity – one mere pairing of a stimulus and a response – is sufficient for learning. Guthrie's theory and its successor, the statistical learning theory of Estes (1950), are the most rigorous variants of an unconstrained Law of Contiguity.

Empirical Departures from the Omnipotent Law of Contiguity

One of the most important variables in the empirical evaluation of the Law of Contiguity has been the interstimulus interval (ISI), the time elapsing from the onset of the conditioned stimulus (CS) until the onset of the unconditioned stimulus (US). The Law of Contiguity predicts that conditioning should take place when CS and US are presented in close temporal proximity. Empirically, however, reliable occurrence of conditioning has repeatedly been observed even when CS and US are separated in time such as in trace conditioning (Pavlov, 1927) or taste aversion learning (Garcia, Ervin, & Koelling, 1966). These observations put a heavy burden on the omnipotent Law of Contiguity.

To go from bad to worse, research suggests that little or no conditioning occurs at ISIs close to zero (e.g., Bernstein, 1934) and that conditioning does not occur equally well at all ISIs. The optimal ISI is the interval at which conditioned responding is at a maximum, whereas longer and especially shorter intervals lead to lower levels of conditioned responding (reversed u-shape). The duration of the optimal ISI is influenced by several factors (for an overview see Gormezano & Kehoe, 1981), for example the response system being conditioned, gradients of inhibitory and excitatory strength along the time axis, and the proportion of reinforced and non-reinforced trials. But even if these factors are kept constant, the optimal ISI varies with the difficulty of the conditioning task. In addition, the optimal ISI is considerably smaller in reinforcement schedules with only one CS than in schedules that require discrimination between two CSs, one being paired with a US and the other one being unpaired (Gormezano & Moore, 1979; Hartman & Grant, 1962).

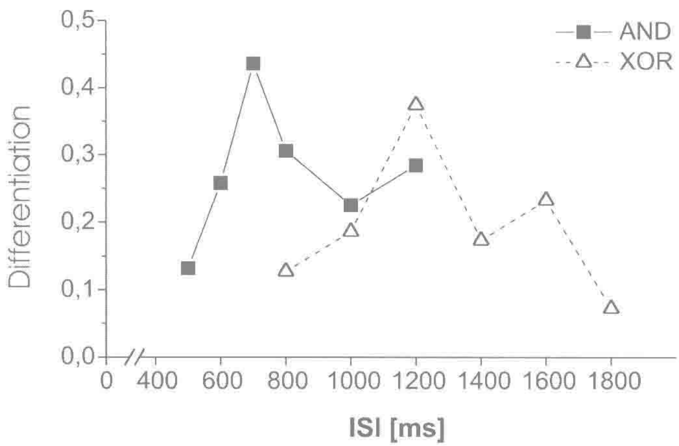

Figure 1. Asymptotic eyelid response differentiation for conjunction (AND) and exclusive disjunction (XOR) in the experiments of Kinder and Lachnit (2002). Each data point resembles response differentiation averaged across the second half of trials. (Adapted from Kinder & Lachnit, 2002).

Even more, in a differential eyelid conditioning study with humans (Kinder & Lachnit, 2002), where all the variables just mentioned where kept constant across groups, we nevertheless observed quite different optimal ISIs. There were 96 trials (48 followed by an airpuff: +; 48 without an airpuff: -) of four different CSs (combinations of dark blue letters on a white screen, e.g., A and B, being either present or absent). Two groups of participants had to solve one of two discrimination problems each, based on the logical rule of conjunction (AND: AB+, AnonB-, nonAB-, nonAnonB-) or exclusive disjunction (XOR: AB-, AnonB+, nonAB+, nonAnonB-). Although this was the only difference between groups, the optimal ISI differed by 500 ms (see Figure 1). Furthermore, even at optimal ISIs the amount of differentiation differed.

Theoretical Attempts to Retain the Law of Contiguity

One possibility to redeem the Law of Contiguity in the face of successful trace conditioning and ISI effects is to assume that a stimulus trace bridges the empty interval between the offset of the