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Space and time: the fabric of thought and reality

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> Space and time are modes by which we think and not the conditions in
> which we live.
>
> – *Albert Einstein*

Since the beginning of sentience, the fabric of reality has been the subject of intense curiosity, and the twin concepts of *space* and *time* have figured prominently in the thinking of individuals of various intellectual persuasions. Understanding in science has advanced significantly through the postulates that underpin coherence and precision in the representation, and measurement, of space and time. These advances have formed the bedrock of the development of many disciplines. However, until the latter half of the nineteenth century many properties of space and time were assumed and therefore remained unquestioned. For example, the implicit acceptance of concepts such as *absolute space* (a coordinate system at rest, relative to which all inertial frames move at constant velocity) and *absolute time* (a universal time independent of any "clock" or mechanism) made most issues related to space and time impervious to empirical investigation and theoretical debate. This state of affairs was robustly challenged by scientists such as Ernst Mach, who among others imagined observers equipped with measuring devices (rulers and clocks) arriving at concepts at odds with notions of absolute space and absolute time.

Many well-known scientists whose work spanned the latter half of the nineteenth century (Mach included) crossed the disciplinary boundaries of physics, philosophy, and vision science. In Mach's thinking on space and time, the observer's sense perception played a critical role. Mach (1890) wrote: "The facts given by the senses . . . are the starting-point and the goal of all the mental adaptations of the physicist [and] the source of every hypothesis and speculation in science." This statement is reminiscent of another by von Helmholtz (1867): "Apprehension by the senses supplies . . . directly or indirectly, the material of all human knowledge . . . there is little hope that he who does not begin at the beginning of knowledge will ever arrive at its end" (cited in Warren & Warren 1968). It is noteworthy that, although in the new conception of space and time to emerge in the early part of the twentieth century the observer played an integral role, the meaning of the term "observer" remained obscure. Thus, although it was implicit that the observer's nervous system was part of the causal framework, one may ask: Which component(s) of the nervous system

are relevant? It is amply apparent that a deeper understanding of space and time, from any point of view, will require a more complete understanding of the observer's nervous system. We suggest that sensory and motor processes in particular not only involve neural representations related to space and time but, more critically, form the basis of the scientist's conception of space and time.

One change apparent in postrelativity thinking is that space and time are no longer thought of as distinct dimensions (Minkowski 1908). We believe it is time for a critical review of separate treatments of space and time in neuroscience and psychophysics. Our unifying efforts are akin to previous efforts by scientists to remove the sharp boundary that is often assumed to exist between perception and action. From a biological standpoint, change and its detection are crucial to the animal's survival. We contend that change, or more generally spatiotemporal events, are the most important stimuli for the nervous system, so it is natural to think of space and time within a unifying perspective.

Change, its detection, and an appropriate response to it are crucial features of all animal behavior. For a single-celled organism, detection of change in the concentration level of some chemical is key to survival. The goal of both internal processes within the animal and its overt behavior in the environment is to maintain homeostasis. For multicelled organisms, change is frequently associated with movement, either because the change itself is due to movement in the environment or because the animal must respond to change with movement. Furthermore, it is well established that change, or any spatiotemporal discontinuity, is a potent stimulus for animal nervous systems. For example, critical information about objects is available at color or luminance edges; stimulus onsets and offsets cause neurons to respond vigorously, whereas static stimuli frequently do not produce a neural response at all, particularly in immature nervous systems; retinal image stabilization (i.e., removal of change) causes visual percepts to disappear rapidly, and so on. Thus, even from a biological standpoint, space and time are naturally connected, and the sharp (intuitive) divide between the two is misleading. It is interesting that a unification of space and time from the point of view of neuroscience and psychophysics seems linked to a unification of perception and action already suggested by a number of notable scientists (e.g., Sperry 1952; Rizzolatti et al. 1997). In conclusion, space and time are connected if one considers moving bodies and clocks from a physical perspective, and when one considers the most significant type of stimulus for biological systems, namely change.

Traditionally, psychologists and neuroscientists treat problems concerning *space* and *time* as more or less two separate and independent problems for investigation. For example, in David Marr's seminal book *Vision,* the spatial aspects of vision were given considerable coverage in stark contrast to the limited analysis accorded to the dimension of time. This is partly because visual pathways are geared to the processing of spatial dimensions. For example, in the domain of space, hyperacuity-level performance (Westheimer 1979) in the two-dimensional plane and in depth appear unrelated to time. Temporal hyperacuity has also been reported (Rose & Heiligenberg 1985). However, such levels of responsiveness require integration over space *and* time. So, the dimension of time is part and parcel of sensory processes even when its role is not apparent or explicitly investigated. Ironically,

integration processes that support many types of performance by sensory systems, hyper-acuity included, are themselves slow. The large latency of visual processes has been reported time and again (Aho et al. 1993).

On the other hand, of the many articles and books published on the topic of time, few give due consideration to spatial dimensions. One reason for separate empirical investigations of space and time could be that the spatial analysis of events on the one hand, and the timing of events on the other, is carried out by highly distinct mechanisms in the brain. The most natural way to analyze the problem of space is in terms of topographic mapping of the receptor epithelia onto the surfaces of both subcortical and cortical structures, whereas the mechanisms that underlie temporal processing of events may be highly varied. For example, timing mechanisms may be localized in cerebellar processes, motor networks involving the frontal cortex, parietal networks, or some combination thereof. Disparate networks responsible for temporal processing are engaged as a function of the task at hand, with different tasks requiring different networks. These processing differences between space and time may limit an integrated treatment of the two.

Nonetheless, there are important justifications for positing that a unified treatment of space and time is both timely and fruitful. For example, many scientists hold that vision cannot be separated from action, and although vision is often discussed without regard to time, action certainly cannot be similarly divorced from time. There is another aspect to considerations of the dimension of time in vision. Visual perception is not instantaneous; time makes its presence felt in visual processing, particularly because there are significant neural delays at the level of phototransduction and the transmission of receptor signals to the primary visual cortex and beyond. These delays have obvious implications for sensory processes engaged with dynamic visual events and for the motor system's ability to utilize the output of these processes for action. Where change is associated with movement in the visual environment, as is frequently the case, neural delays or issues of time directly impact issues of space. Thus, the relevance of time for vision, already well established for research on auditory processes, is beginning to be appreciated.

A unified treatment of time and space is apparent in the list of chapters. One chief methodology employed by researchers to address problems of space and time involves the study of "illusions," particularly when these illusions are related to or caused by actions. It is well known that animals such as humans are subject to a number of "illusions" related to dimensions of space and time. Action related to perception is thus liable to potential errors unless one takes the strict position that parallel neural streams subserve perception and action. It is doubtful, however, that the two streams are completely independent of each other. In the recent past, researchers have identified and scrutinized several important "illusions." The sixty-four-thousand-dollar questions are: Can the nervous system compensate for these illusions to produce accurate behavioral output? Does the nervous system need to compensate for these illusions, or do these illusions actually aid in the production of adaptive behavior? These questions have become more central to the work on space and time in the last several years. Research conducted in response to such questions is the mainstay of this book.

We bring together theoretical treatments and empirical findings from a number of neuro-scientists and psychophysicists with significant experience in the study of space and time. The twin issues of localization in space and time are covered in this book. Two conferences on the topic of Space–Time were key to providing a wellspring of ideas from which this book took shape. The first was titled "Visual Localization in Space–Time" and was held at the University of Sussex (August 2002); the second focused on "Problems of Space and Time in Perception and Action" and was held at the California Institute of Technology (June 2005), as part of the proceedings of the annual conference of the Association for the Scientific Study of Consciousness (ASSC 9). We seek to capitalize on the many fruitful areas of investigation that have emerged in the past several years, and bring together the approaches of scientists who treat time and space as two faces of the same coin (see, e.g., Schlag & Schlag-Rey 2002). The thinking and experiments of researchers working on these topics are presented in a single volume to encourage greater synergism in this exciting field of investigation. This book will achieve its goal if it challenges scientists to bring future questions on space and time under a common umbrella of investigation.

Given that perception is not instantaneous, logic dictates that real-time action must acknowledge and overcome delays inherent in the nervous system. Therefore, we begin with action and the requisite computations of space and time for accuracy in action. Interrogating visual stability in the presence of eye movements has offered insight into the representation of visual space. The late Hitoshi Honda (Chapter 3) deftly analyzes the texture of visual space surrounding a Saccadic eye movement in the presence and absence of visual input. Memory is presented as a cocontributor to vision in maintaining a stable visual world (Lappe, Michels, & Awater, Chapter 4). Using Saccadic eye movements, a case is made for sensorimotor control that requires representations of *both* space and time (Schlag & Schlag-Rey, Chapter 2), whereas a breath of fresh air for psychophysics is presented by the relativistic-like effects of spatial compression and time dilation as a result of shifting gaze (Morrone, Ross, & Burr, Chapter 5). Matin and Li (Chapter 6) make the argument for stability based on a quantitatively precise cancellation function between retinal input and extraretinal position information and the elimination of presaccadic persistence. However, because the underestimation of eye deviation renders compensation via extraretinal signals incomplete, it is provocatively proposed that extraretinal signals are not in the service of compensating prior retinal signals but actually destroying them (Bridgeman, Chapter 7).

What about seeing for reaching? Evidence is sought but none found for object pursuit producing "spatial advanced" representations for overcoming neuromuscular delays (Brenner & Smeets, Chapter 8). At the close of this section the relationship between visual motion and goal-directed reaching is reviewed to conclude that visual motion, although shown to compromise the accuracy of goal-directed reaches, can also contribute to accurate reaching behavior (Whitney, Murakami, & Gomi, Chapter 9).

These initial chapters pivot around representations for action. They are then followed by two sets that focus on temporal and spatial phenomena in perception. We begin with those focused on temporal processing. Going backward in time, a.k.a. temporal antedating, is offered as an account of saccadic chronostasis, or the perceived temporal lengthening

of a visual stimulus postsaccade (Yarrow, Haggard, & Rothwell, Chapter 10). Verstynen, Oliver, and Ivry (Chapter 11) measure temporal perception as a function of self-initiated actions to provide compelling evidence for anticipation not only rendering accuracy in action (nothing particularly new there) but critically also affecting our percepts. The result of an investigation into the influence of spatial configurations on perceived durations becomes the basis for spatial priming in temporal kappa effect (Aschersleben & Müsseler, Chapter 12). Then we go on to the perennial problem in vision of establishing coherence out of disjointed sources of information, that is, binding. Temporal binding of visual information has become an intensely researched and fiercely debated enterprise. Clifford (Chapter 13) incisively analyzes both empiricisms and theoretical positions in this burgeoning area of research. Latency differences (Arnold, Chapter 16) and time markers (Nishida & Johnston, Chapter 17) are contrasted with a view that feedback from higher cortical areas to primary visual cortex account for perceived asynchronies. Concordant with this view is the proposal of a high-level brain program for timing based on data for perceived synchronicity of pairs of motion stimuli and pairs of motion and flicker or motion and flashed stimuli (Lankheet & van de Grind, Chapter 18). Eagleman (Chapter 14) attempts to square the issue of processing speed and perceived time by suggesting that the brain computes percepts by waiting for the arrival of the slowest signals. The perception of simultaneity is considered a productive approach to how the brain accurately time stamps events when the process of time stamping itself takes time (Harris, Harrar, Jaekl, & Kopinska, Chapter 15).

Time translates into space. Kerzel (Chapter 19) and Maus (in Maus, Khurana, & Nijhawan, Chapter 27) both bring the classic findings of Fröhlich, Rubin, and Metzger to a wider academic community: The original findings were published in German and remained inaccessible to many interested in the current debates on the spatial and temporal aspects of motion perception. Kerzel attempts to reconcile the Fröhlich effect with the newly discovered onset repulsion effect, whereas Hubbard (Chapter 20) organizes the various theories and models of representational momentum. Based on their assumptions and prowess in terms of accounting for data, Nagai, Suganuma, Nijhawan, Freyd, Miller, and Watanabe (Chapter 21) divvy up representational momentum and the flash-lag effect based on different conceptual influences. The chopsticks illusion offers a window into visual parsing and is used to interrogate whether spatial offsets in the flash-lag effect are computed after motion parsing. Both the chopsticks illusion and reversed phi suggest that the flash-lag effect is a function of motion processing before perception of moving objects (Anstis, Chapter 24).

No understanding of a perceptual phenomenon is complete without a consideration of the role of attention. Baldo and Klein (Chapter 23) carefully scrutinize attention shift delays as modulators and causes of perceived spatial offsets between moving and stationary flashed stimuli. Jancke and Erlhagen (Chapter 25) offer a computation model with biological underpinnings that brings under a shared canopy the Fröhlich, flash-lag, and representational momentum effects. Changizi, Hsieh, Nijhawan, Kanai, and Shimojo (Chapter 26) extend the conceptual canvas further to account for whole classes of geometrical illusions based on the visual system's estimate or "guess" as to the visual syntax of the next moment.

They argue that the visual system's foreknowledge, anchored in exploiting the ecological regularity of forward motion, permits latency correction when forward motion is visually implied. The section closes with an evaluation of various accounts of the flash-lag effect such as differential latency (Kafaligönül, Patel, Öğmen, Bedell, & Purushothaman, Chapter 22), postdiction, and attentional cuing, both theoretically and in light of new data on unpredictable motion (Maus, Khurana, & Nijhawan, Chapter 27).

In the end, one must tackle visual awareness. Enns, Lleras, and Moore (Chapter 28) suggest that perceptual continuity, in the presence of chaotic spatiotemporal inputs, is preserved by operating at the level of objects – object updating. Evidence from visual masking, the flash-lag effect, priming, and perceptual asynchronies is presented in favor of this account. The final two chapters take a stab at the contents of awareness with VanRullen, Reddy, and Koch (Chapter 29) relating the continuous Wagon Wheel illusion to the underlying quasi-periodic brain processes and Bachmann (Chapter 30) offering streamed/continuous stimuli as privy in terms of visual awareness.

We have attempted to be broad and inclusive in our coverage. We hope the diversity of positions adopted in the following chapters, the variety of perceptual phenomena investigated, and the numerous approaches to synthesize first and foremost inform the audience with state of the art in this field. For the future, we look forward to this collection rendering a platform for the problems of space and time in perception and action upon which the next generation of science can build. We tip our hats to Captain Kirk by closing with the thought that space–time is the final frontier in the exploration of our visual world.

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Part I

Time–space during action:
perisaccadic mislocalization and reaching

2

The internal eye position signal, psychophysics, and neurobiology

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Summary

"Real-time sensorimotor control requires the sampling and manipulation not only of parameters representing space but also of those representing time. In particular, when the system itself has inherent processing delays, it invites a situation in which sampled parameters from a peripheral sensor may no longer be valid at the time they are to be used, due to the change in state that took place during the processing delay" (Dominey et al. 1997). In this chapter, we focus on the situation in which a visual stimulus is flashed near the time of a saccade, and the subject's task is to orient the eyes toward the site where the stimulus has been. To perform this task in complete darkness, the subject's brain has to rely on only two signals: retinal error signal and internal eye position signal (iEPS). This is one of the most interesting situations in which the brain has to compute something in the face of specific physical odds (e.g., very long latencies), and we have some hints on how it proceeds. We analyze the time course of the iEPS – which appears quite distorted – using electrical stimulation of brain structures, instead of natural visual stimuli, to provide the goal to be localized. Different hypotheses are then discussed regarding the possible source and possible neural correlate of the iEPS.

Although vision is usually thought of as a continuous process – continuous in space and time – it is periodically interrupted by rapid eye movements called saccades. These are the movements you make while reading this text. Saccades are necessary because the limited part of the world you see well is the tiny one projecting its image on your fovea. In the retina, only the fovea has a resolution comparable to that of modern digital cameras. Therefore, when a new site of interest appears, you need to reorient your retinal fovea. This may happen several times per second. Each time, even though you don't realize it, your vision becomes transiently vulnerable (much more than during a blink, Deubel et al. 2004). There are several kinds of visual disruptions that may occur at the time of saccades: first, a relative, temporary blindness to changes in the environment (particularly displacements of visual objects) called saccadic suppression (Dodge 1900; Diamond et al. 2000); second, a shift of the apparent location of visual stimuli briefly presented near the time of saccades (Matin & Pearce 1965; Bischof and Kramer 1968; Pola 1976; Mateeff 1978); and third, an apparent bringing closer together of simultaneous visual stimuli, described as space compression (Ross et al. 1997). These three phenomena have about the same time course. As they start appearing for stimuli presented well before saccades (e.g., more than 100 msec) and fading

out for stimuli presented well after saccades (e.g., more than 100 msec), clearly their cause cannot be simply mechanical: they cannot be due to the displacement of the eyeball (and the retina with it).

This chapter deals with the perisaccadic mislocalization of brief stimuli that, in darkness, consists in an illusory shift of their position. There are two ways to reveal and measure this shift: one method is perceptual (e.g., locating the test flash with respect to a ruler or a landmark), the other is targeting the visual stimulus (e.g., looking or pointing to the site where it has been). Although initially the results obtained by these two methods were thought to be different (Hallett & Lightstone 1976; Hansen & Skavenski 1985), most recent studies indicate that both methods produce equal mislocalization (Honda 1989, 1990; Dassonville et al. 1992a, 1995; Bockisch & Miller 1999; Boucher et al. 2001). When a shift is observed, its direction and amplitude depend on the timing of the test stimulus. For stimuli presented before the saccade, the shift is in the direction of the saccade. For stimuli presented during the saccade or later, the shift decreases and, for some subjects may even reverse to the opposite direction (e.g., Honda 1990). Complete darkness provides the best condition to demonstrate the shift because, were visual landmarks available, the brain would rely on these cues to recognize spatial relationships (see Bridgeman, this volume), and the phenomenon of compression would also arise (Ross et al. 1997). It is true that mislocalization can still exist in the presence of visual cues and even in the absence of saccades (for instance, when stimuli are moved at saccadic speed in front of an immobile eye, e.g., Ostendorf et al. 2006). But here we are concerned with the saccadic mechanism. Therefore, ideally, the demonstration of perisaccadic shift should be designed with only one test stimulus: preferably a very brief flash and nothing else (no point of fixation and no saccade target). In such an experiment, Dassonville et al. (1995) flashed a point-like stimulus for 2 msec near the time of saccades that subjects had learned to perform upon auditory command. Subjects were instructed to make a first saccade of a given dimension in a specified direction, and then a second saccade to the unmarked site of the flash. In this experiment, targeting was used to measure the mislocalization because any visual cue (e.g., ruler) was to be avoided. A mislocalization of the site of the flash was then observed, which could reach a maximum shift, up to 70% of the first saccade amplitude, when the flash occurred just before saccade onset.

To understand why this mislocalization happens, one should realize that the visual system is slow. It is so slow that it takes more time for visual information to reach the brain than it takes to make a saccade. Therefore, if a flash occurs just before a saccade, the signal that it has occurred is decoded in your brain only after that saccade is completed. How could you ever locate the flash? You could, but only if your brain knows exactly how your gaze was oriented at the instant of the flash. For this purpose, the brain must be able to access – at the proper time – a signal faithfully representing the time course of the saccadic displacement. Is such a signal available? Imagine that you look at a wallpaper that shows a uniformly repetitive pattern of blackberries: how do you know which blackberry you are looking at? Possibly one of the blackberries is perceived with a higher resolution, but this does not help much. You cannot discriminate any blackberry by its visual characteristics because
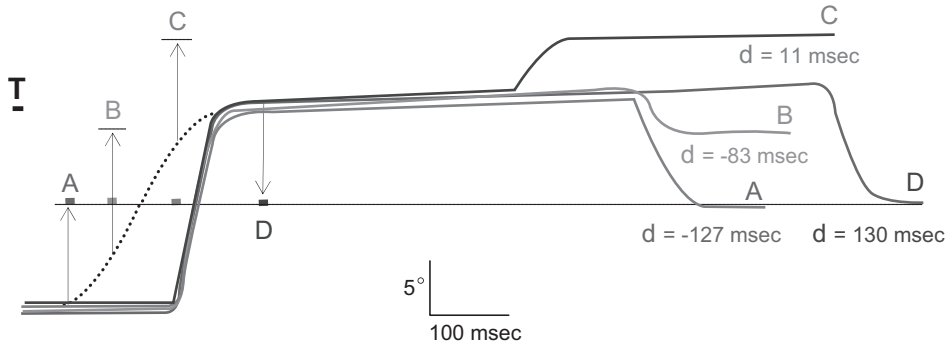
Fig. 2.1 Determination of the iEPS using stimulus mislocalization in complete darkness. Four trials with traces of horizontal eye position recorded by a magnetic scleral coil in a human subject. Two brief stimuli were flashed: T and either A, B, C, or D at indicated times relative to the onset of the saccade to T (= 0 msec). The subject was instructed to make a saccade to T and then to the site where the second flash (A, B, C, or D) was perceived. The delay of the second saccade was not imposed and, therefore, varied in different trials. Black vertical arrows represent retinal vectors. Dotted black curve represents derived iEPS signal. Usually data in such experiments are much noisier than suggested by plotting just a few points as here (see Fig. 2.2 Visual). Other details are described in the text.

all blackberries are the same, and all are at equal distance from each other. Yet apparently you can single out the one you are looking at, as proven if you are allowed to point with your hand (even if you do not see your hand). This seems to imply that there is some sort of a virtual crosshair in your brain that indicates to you where you look. Although this crosshair is invisible, its position is available in terms of its coordinates with respect to the head (and it will be readjusted if you wear prism goggles). This is the internal (or inferred) eye position signal (iEPS). As introduced here, this notion is abstract; we are not referring to any particular biological signal that has yet been identified.

In the absence of other visual cues, the brain can calculate the position of a stimulus briefly presented during a saccade only by adding the iEPS to the retinal position of the stimulus. Absent any internal delay, this addition would be performed in "real time" and the localization of the stimulus could be correct. If it is not correct, we may assume that the iEPS is in error, and from this error we can calculate the iEPS time course. This calculation, explained by the example of Fig. 2.1, is the reverse of the operation specified at the beginning of this paragraph, that is:

$$\text{iEPS} = [\text{retinal position minus saccadic displacement}]$$

Figure 2.1 shows, superimposed, four traces of the horizontal eye position of a subject trying to look successively at the sites of two briefly flashed targets in complete darkness. It is essential that the stimuli be brief because mislocalization diminishes with long stimuli (e.g., ≥50 msec; Vliegen et al. 2005). This is not surprising: if stimuli are too long, they start too soon before the saccade (i.e., they are no longer really perisaccadic), or they continue