

Why the past is sometimes perceived, and not only remembered

Helge Malmgren

Department of Philosophy, Göteborg University

e-mail: *helge.malmgren@phil.gu.se*

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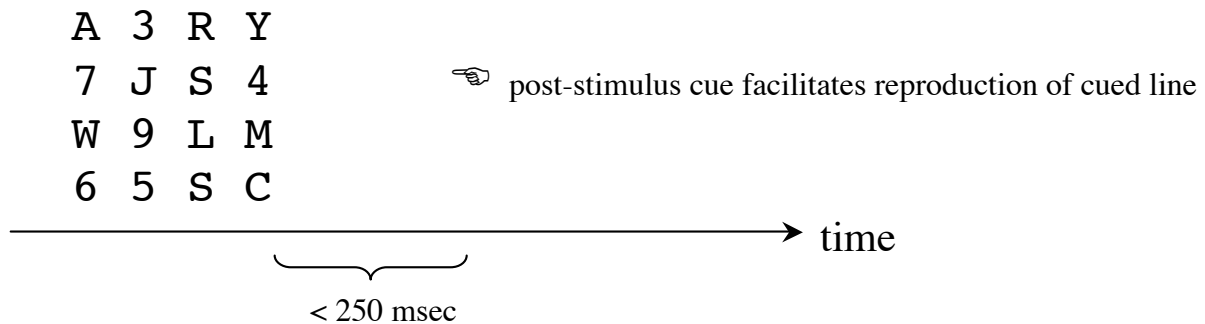
Updated abstract

This paper first advances and discusses the hypothesis that so-called “iconic” or (for the auditory sphere) “echoic” memory is actually a form of perception of the past. Such perception is made possible by parallel inputs with differential delays which feed independently into the sensorium. This hypothesis goes well together with a set of related psychological and phenomenological facts, as for example: Sperling’s results about the visual sensory buffer, the facts that we seem to *see* movement and *hear* temporal Gestalts, and the fact that we sometimes seem to hear sounds only after they have stopped. In its most simple form, and formulated in the somewhat misleading information processing idiom, my hypothesis says that each one of a number of parallel input lines with different delays feeds into a spatially separate sensory unit. The set of such units then holds information about the immediate past in what one might call a “chronotopic” sensory map. This contrasts with the idea (common in sensory buffer theory) that the received sensory information is kept (while possibly decaying) in the same unit for some time after it occurred. The hypothesis also contradicts the theory that all sensory information passes through the same unit but is then successively passed through a unidirectional chain of separate units, where the past experiences then become represented (the shift register hypothesis). The main advantage of my theory, beside the natural explanations it offers for the above-mentioned kind of phenomena, is that it postulates a parallel – and therefore robust – rather than a serial mechanism for the registering of temporal information. It can of course easily be modified to fit more complex models of the sensory cerebral code(s) as well as of the chronotopic representation as such.

In the second part of my poster, I advance a corresponding hypothesis for those motor commands which control brief movements. At closer inspection, most so-called “ballistic” movements do not seem to be truly ballistic (in the sense in which the movement of a cannonball is so) since the brain must exert some kind of feedforward control over the later part of their trajectory. I suggest that this control is at least sometimes realized by means of differentially delayed output from a chronotopic representation of successive segments of the movement. Not only could this be a biologically natural way of ensuring efficient adaptability of the movement; the hypothesis also explains the not uncommon experience of “seeing the whole movement laid out in advance” when it is initiated.

Historical landmarks Three hundred years ago, German philosopher-physicist Leibniz remarked that we often seem to hear a sound only after it has stopped (1). But how can we notice the stopping if we did not hear the sound? Leibniz answered this question by introducing the notion of “small perceptions”. Unnoticed sounds are perceived, although not fully so, and through this “small perception” we get informed about their ending. However, Leibniz did not discuss at length why we then seem to get a retroactive full perception of the sound. Around the previous turn of century, philosophers belonging to such diverging traditions as empiricism and phenomenology took an interest in this issue. Several important thinkers, among them William James (2) and Bertrand Russell, argued that we could not have a concept of time without having had a direct, original experience of time. The phenomenon of immediate memory, or “retention” as phenomenologist Edmund Husserl preferred to call it, was often supposed to constitute such an original experience of time – a perception of time.

Sperling’s experiment in 1960 (3), and many similar experiments which followed, seemed at the time to establish beyond reasonable doubt the existence of “sensory buffers”, placed between the sense-organs and short-time memory proper in the sequence of information processing. Sperling showed that the reproduction of briefly presented visual stimuli could be facilitated by cueing their location shortly *after* they had ended; schematically:



The sensory buffers were almost always conceived as species of *memory*, not of perception. They were thought to *retain* sensory information after it had already been registered. Hence they did not offer the perceptual windows into the past that some philosophers had envisaged. This was emphasized by a later change of terms from “sensory buffer” to “iconic” and “echoic” *memory* (4). – Among recent research one should mention the findings (*pace* Sperling) that proper cueing after the end of the first stimulus can eliminate the phenomenon of visual change blindness (5), and that (*pace* Leibniz) the so-called mismatch negativity in auditory evoked potentials is seen also in pre-attentive auditory processing (6).

Temporal Gestalts Melodies, melody fragments, heard sentences, heard parts of speech all constitute examples of *auditory temporal Gestalts*. It is here of importance to distinguish between Gestalts of very short and of longer duration, corresponding to the time-scales of the sensory buffer and short-term memory proper, respectively. Just after hearing the initial five bars of Beethoven's Fifth,

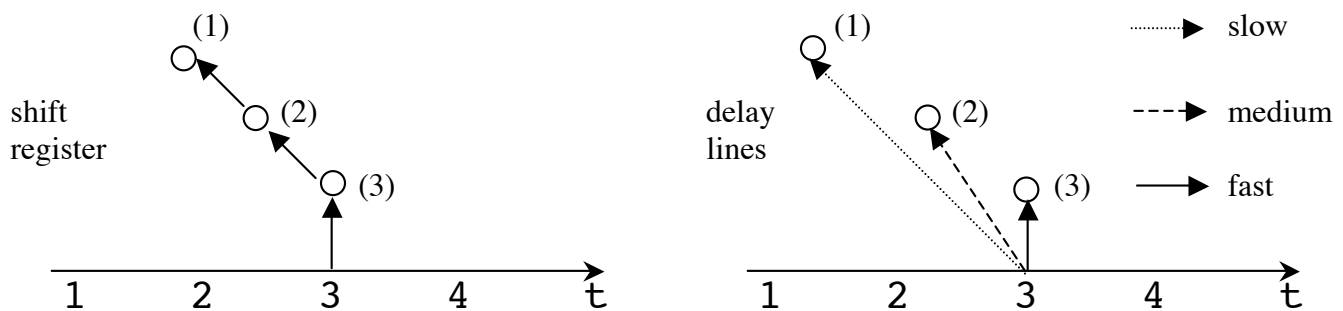


you will probably have the whole segment before your “inner ear” as a auditory whole. (On the basis of it, you may for example form an aesthetic judgment about the ability of the conductor to connect the five bars in a proper way.) But before that, you heard, noticed and appreciated other Gestalts, for example at the end of the first bar. Most probably, the larger Gestalt was influenced by the smaller one through short-term memory. If you go on analyzing your musical experience, you may even remember that already after the first chord, you noticed that its onset was very nice. Now the final Gestalt appears to be a very complicated product of many short-term memory operations upon earlier, successive Gestalts. (I will not discuss the role of anticipation here, in order not to complicate things more.)

I will now argue a point which several readers may find trivial, but which has important consequences for my thesis: namely, that there are Gestalts which are *not* products of short-term memory proper, but belong to the sensory buffer. The smallest musical segments which you can find in your introspective analysis of your Beethoven experience (maybe that related to the “onset” experience is an example) are candidates for being such sensory buffer Gestalts. But let me take a more convincing example: if you suddenly and unexpectedly hear a brief downwards-sliding tone, you will not notice it until it is over, just like in the experience so well described by Leibniz. Hence there will be no possibility, during the occurrence of the tone, for attention to even try to keep its parts in short-term memory proper. However, you will certainly hear it – afterwards – as sliding. Hence there are temporal Gestalts in the sensory buffer. Another example is hearing a small segment of speech. Unexpectedly hearing an initial “p” being pronounced is usually an event that takes places wholly within the sensory buffer.

Brief seen movements offer yet other examples, but I do not have enough room to discuss seen movements further in this poster.

How does the sensory buffer “retain” a temporal Gestalt? The fact, if it is a fact, that there are temporal Gestalts within the scope of the sensory buffer, makes it urgent to analyze further the question of how “sensory information” is “stored” and “retained” in the buffer. Two considerations make it implausible to think of these processes in terms of a single-unit representation. (Note that I skip all complications introduced by for example tonotopic coding, since to be able to discuss the nature of the time-code in a simple way, I have to abstract from all other aspects of the cerebral code.) To suppose that the sensory signals which correspond to the parts of a brief sliding tone are all represented in the same unit (again, in the abstract sense) means that we present the brain with a difficult decoding problem. For the signal *is* decoded: we hear a clear difference between upwards-sliding, downwards-sliding and constant brief tones. This is actually difficult to explain in terms of any kind of integration-followed-by-decomposition process occurring in the same unit. A computationally much simpler solution is some kind of *chronotopic representation* in the sensory buffers. With this I mean that different temporal parts of the sensory input are represented in different neural units. A chronotopic representation can be of any resolution, but if it is realized by means of neural units, the resolution must be finite. (Do not confuse the question about the resolution of our temporal representations with another issue about resolution: whether the “stream of consciousness” is *itself* a sequence of discrete events (7), and if so, what duration these events have.) A chronotopic code can be created from input either by a shift register or by input lines with different delays. Consider a chronotopic representation at time = 3:



The natural heir of the standard “retainment” model of the sensory buffer is of course the shift register theory. However, I think that the delayed input model much better explains the experiential features of “hearing afterwards”. But my main argument is that a parallel mechanism is more robust than a serial one. If the sensory buffer is a shift register, information will be lost if the chain is broken anywhere. This, of course, is what happens when items are lost from short-term memory proper. With parallel input lines, the information can be recovered later.

What is memory and what is perception in speech perception? There is an important methodological difficulty involved in introspective studies of sensory buffers. It is due to the fact that the sensory buffers are not alone in using intrinsically iconic or echoic representations, i.e. a sensory or quasi-sensory code. Dreaming, daydreaming and all other forms of so-called “mental imagery” use sensory code as well. Thus, introspective studies may be difficult to interpret: the fact that we still “hear” the first tone of Beethoven’s fifth when the fifth bar ends does not entail that we still *hear* it (i.e. that it is within the scope of the auditory buffer); it could as well be a case of lively short-term memory. The definition of a sensory buffer, as opposed to short-term memory proper, must therefore rely on a functional specification rather than on a phenomenological one. Such a functional definition should have to do with the extent to which the neural activation in a given part of the chronotopic map depends on the activations of its other parts and on feedback from “higher” brain areas, rather than directly on incoming signals from the sense organs. There are several options available for an exact definition but I will not try to choose between them here.

A controversial and unresolved issue in the debate over the auditory sensory buffer (echoic memory) is whether its duration is similar to that of the visual buffer (around 250 msec) or considerably longer (more than 2 seconds). It might be the case that the issue has been confused because of the methodological difficulty mentioned above. It is comparatively more easy to intentionally form a lively “auditory image” than to form a lively visual one, so maybe short-term auditory memory is prone to be misclassified as “echoic”. Neither is it easy to interpret the objective evidence. Ionannides et al (8) argue from magneto-encephalographic data that the echoic memory time (EMT) of the male left hemisphere is greater than the EMT of the right. However, this interpretation depends on the implicit assumption that the oscillatory source which produces the late components of the auditory evoked response which they investigate is “sensory” in nature (in the above functional sense), although it lies outside the primary auditory cortex.

My argument against the authors’ interpretation notwithstanding, I believe that they are essentially right. I tend to think that when listening to a human voice, we can actually retrospectively *hear* the past two seconds or so. On the other hand, this extended sensory buffer may well overlap in time with the operation of short-term memory proper, sometimes producing mixed effects.

Varieties of motor control A movement can be under either feedback or feedforward control, or both. If external and organismic input during the execution of movement plays no role for the shaping of a certain control signal, control is feedforward. Feedforward control is compatible with adaptation of the controller by means of endpoint feedback. At one extreme of the spectrum of movements under feedforward control lie so-called “ballistic” movements.

Motor control, and especially feedforward control, is often said to presuppose that the organism has some kind of (approximately correct) internal “model” of itself and/or the environment. Not only feedforward, but also feedback control in the narrow sense (i.e., in-trajectory control based on external signals), may seem to need such a model: surely the system must “know” what kind of endpoint error the external signal predicts and how it should act to minimize this error? When it comes to feedforward control, a distinction is usually made between “forward” and “inverse” models. Having a forward model is the same as “knowing”, for each control signal in a set, which signal leads to which result; while an inverse model specifies which control signal to choose given a certain desired result.

Now, it is not immediately obviously what should be meant by saying that a system – say, the brain – *possesses a model of so and so*, or that it *knows so and so*. Philosophers have long argued that such “intentional” descriptions may be underdetermined by the available empirical data about the behavior of a system. It seems that any behavior which issues from a correct model and the proper choice of control signals could also be explained by postulating a systematically erroneous model and compensating, “wrong” signals. If, on the other hand, successful feedforward control is taken as a *sufficient* criterion of the possession of an internal model, then the internal model hypothesis has no explanatory value.

However, these objections are not valid for one sense of “internal model”, namely, *internal simulation*. If what is meant is that the brain – using, among other things, corollary discharge from motor areas – produces neural activations which then act as functional substitutes of sensory signals, the statement that the system possesses a correct model of the world has a clear and empirically verifiable sense. Feedforward control by means of such an internal model or simulation means that the neural activations which simulate real input are used as *virtual feedback*, i.e. as substitutes for in-trajectory external or organismic feedback (cf. walking in a completely dark but well-known room and stopping when one “sees” that one is close to the wall).

Are “ballistic” movements really ballistic? Brief, rapid and relatively simple movements, such as quickly extending the forearm in the elbow joint, are often classified as “ballistic”. The origin of the latter term is of course the science of ballistics – how to throw cannon balls at the enemy. A cannon ball is thrown by giving it a certain movement impulse at start; no in-trajectory control (either feedback or feedforward) is needed. On the other hand, end-point feedback is used to calibrate the original impulse. So, ballistic movements in the strict sense are extreme cases of feedforward control.

Are brisk movements of the forearm ballistic in the cannonball sense? If one takes a look at some recent examples of research on so-called “ballistic movements” (9), it may not seem so. Not only do the descriptions of the movements suggest both initial and terminal control (“quickly rotate your forearm to this position”), but the EMGs turn out to have several peaks corresponding to initial and terminal activations of muscle groups.

On the other hand, it is hard to avoid the conclusion that the control of such “ballistic” movements is feedforward in nature. It is generally agreed that in-trajectory external or organismic feedback is too slow for this purpose. I will also assume that virtual feedback, as defined above, is too slow in virtue of its functional closeness to real feedback. If this is so, the controller does not depend on any signals which arrive during the movement for shaping its control signals. In other words, it must be possible for the brain to send a sufficient control signal at the start of the movement. This would mean that the movement is ballistic in the narrow sense, after all.

What may mislead us to think the opposite is a simplified conception of the initial signal, modeled on the cannonball example. We cannot move our arm to a certain position by just throwing it away at a certain speed and in a certain direction. But perhaps we can get it there by means of another initial signal – only.

Supposing that this is how things work with “ballistic” motor commands, how is the initial signal coded? A crucial issue for the thesis of this poster is whether an explicit representation of time is involved or not. This has been investigated both theoretically and empirically in a recent paper by Karniel and Mussa-Ivaldi (10) which I will now discuss in some detail. For another contribution to the debate, but focusing on the timing of rhythmic movements, see (11).

State or time representations? The future state of a dynamic system at given moments can sometimes be easily controlled through manipulations of a physical parameter. If, for example, you want a pendulum to be at its opposite highest position ten and twelve seconds from when you release it, you can successively adjust the length of the pendulum until it behaves in the desired way. Using the “internal model” idiom, one can say that it is here comparatively easy to find an inverse dynamical model by sampling the forward model and correcting for the errors by a transparent algorithm. For somewhat more complicated systems this is often not possible in practice, even if all their future states are indeed fully determined by the initial state. One only has to think of the chaotic behavior of a periodically forced pendulum to realize this. In such cases we need in-trajectory control signals to achieve the desired result. And if we are talking about pure feedforward control, such signals must not rely on measured or estimated errors.

An obvious alternative for controlling the periodically forced pendulum is to use time explicitly. In the example it could simply mean that we move the pendulum manually to the desired position just before the 10 and 12 seconds have passed and hold it there for enough long. Not that this is a very sophisticated control strategy, but it does illustrate my point that control which is difficult using state representations may be easy using time. Hence, given the complexity of the behavior of even simple neural circuits, one might expect the CNS to use time explicitly for at least some control tasks.

In an ingenious set of experiments on rapid movements of the arm in varying force fields, Karniel and Mussa-Ivaldi (10) found that the subjects could easily adapt to the fields when these were uniquely correlated with movement parameters. But no adaptation occurred when the fields varied over time independently of the state of the hand. The authors take this as showing that an explicit time representation is *not* used in the control of these movements. I admit that their findings are a piece of counterevidence against my theory. But on the other hand I think that a distinction has to be made between *using a temporal code in controlling a behavior*, and *using purely temporal information to adjust the controller*. As I see it, it might well be the case that brief movements are programmed as sequences to be stepwise executed at pre-determined moments of time, but that adjustments of the program are based on endpoint feedback only. And even if this endpoint feedback has to presuppose some capacity to use basic temporal information (such as *too late/too early*), this capacity need not, by far, be as advanced as that required for keeping full track of a periodic change.

How to implement a temporal motor code When a human wants to program a digital computer to use an explicit time representation for a control purpose, the straightforward way is to create a lookup table or a general function linking points in time with control signals. One more thing is needed, *viz.* that the computer has a time-keeping mechanism, usually called a “clock”. Well, how might the nervous system realize the temporal code necessary for the proposed kind of control? A common answer to this question, when put in general form, is that the brain uses some kind of “internal clock” based on neural oscillators. However, there are several objections to this idea as applied to control of “ballistic” movements. First, neural oscillator rhythms are not quite stable since they are influenced by both external and organismic stimuli. Therefore they may not be sufficiently exact timekeepers to make precisely tuned ballistic movements possible (for example, in attacking a prey or fighting a conspecific rival). Second, neural clocks do not have a display – or to speak less metaphorically, coupling time to actions by means of oscillators is not a trivial task. A ballistic action can start anywhere in the oscillatory cycle, so the control strategy needs a way of estimating intervals which is independent of the starting point in the cycle. So, we seem to be back in a state-code problem.

Both these problems could possibly be solved by using a chronotopic motor map with differentially delayed output lines. This would mean that the temporal segments of the movement are represented in parallel, and that the motor commands for all the segments are sent simultaneously. The correct order and timing of the movement segments are guaranteed by the output delays which define the chronotopic code. These output delays may be more stable than cycle times in systems of neural oscillators, and temporal fine-tuning of a movement is straightforward in a chronotopic map. If we failed to catch the ball since we closed our grip too late, we just tell our hand to “close the grip a little earlier next time”. The motor command representing the closing of the hand is then moved in the chronotopic motor map by a distance which corresponds to the desired temporal change.

To avoid all misunderstandings, I want to emphasize that the proposed theory is quite neutral on other issues concerning the coding of movements, for example, whether neurons in the primary motor cortex code for individual muscle actions, for whole movements, or for neither (12), or even whether neurons or fields embody the code. The chronotopic motor map is suggested as another *dimension* of the cerebral code, whatever its other features may be.

Acknowledgements

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