

## Time perception: Brain time or event time?

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**Recent experiments show that synchronous events can appear to an observer to occur at different times. Neural processing time delays are offered as an explanation of these temporal illusions, but equating perceived time with processing time leads to some thorny philosophical problems.**

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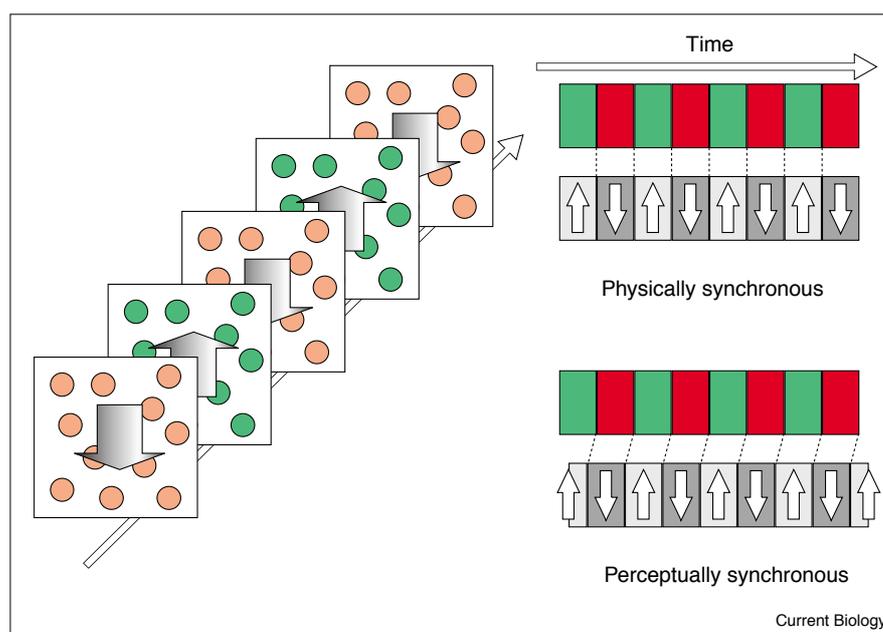
Our sense of extension in space can be traced to the orderly pattern in which receptors sample the retinal image, but there is no equivalent orderly arrangement of receptors designed to register temporal patterns. This makes space perception and time perception different from the outset, and renders mysterious the neural mechanisms by which we sense the time course of events. We can judge whether two events occur at the same time, or which of two events occurred first, but these temporal judgements are not universally reliable, particularly when the events

occur very close together in time. Psychophysical experiments in which subjects were asked to report whether reversals in colour of a patch of dots occurred at the same time as reversals in the direction of movement found that the motion changes had to lead the colour changes by around 80 milliseconds for the two events to appear synchronised [1,2]. This has led to the idea of a distributed asynchronous consciousness, resulting from the neural activity in functionally distinct areas of the brain, each of which spawns its own unique microconsciousness [3–6]. An intriguing new study by Arnold, Clifford and Wenderoth [7], recently published in *Current Biology*, finds that measurements of the colour-contingent motion aftereffect are also consistent with an average delay of 80 milliseconds in motion processing.

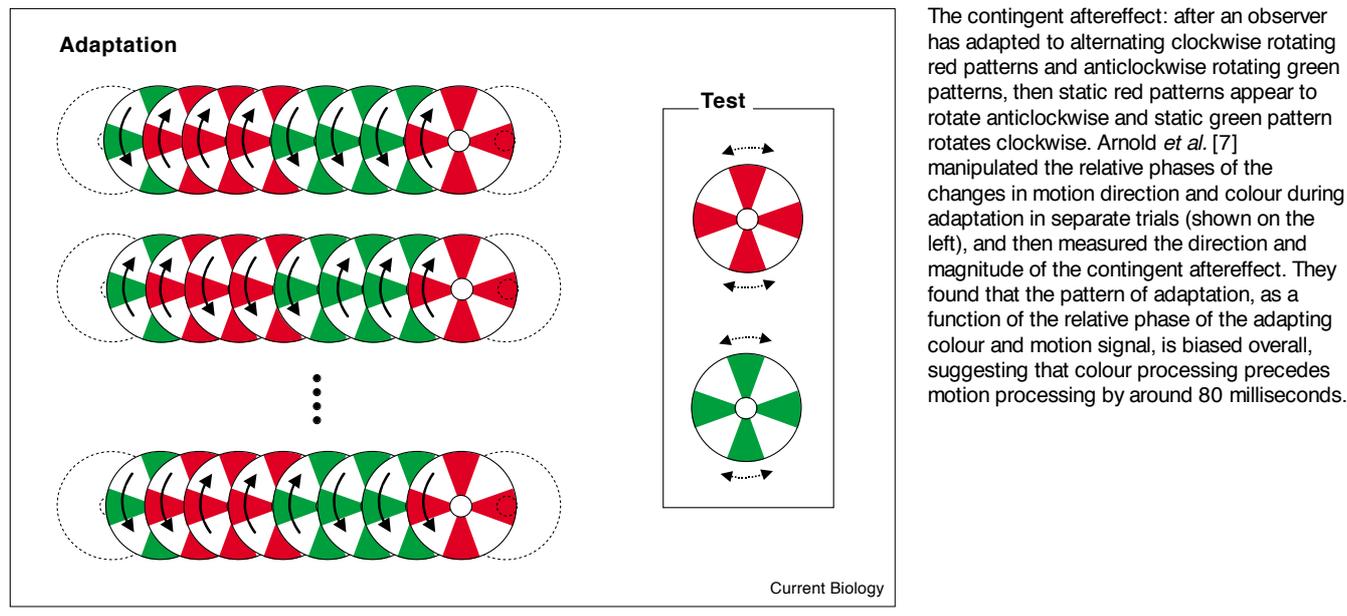
The idea of functional specialisation of the human visual cortex, originally based on reports of specific cognitive deficits after brain damage [8], has in recent years been confirmed by direct imaging of the functioning human brain [9]. Our modern view of the brain is based on the notion of a collection of interacting functional units. This raises the question of how these modules give rise to our inner experience, usually portrayed as that of single observer looking out on an external world. There does not appear to be any particular region of the brain that performs the

**Figure 1**

Green dots moving upwards and red dots moving downwards do not seem to change in synchrony. The changes in direction have to precede the changes in colour by around 80 milliseconds to achieve temporal binding. The arrow indicates the direction of time past.



**Figure 2**



function of gluing together or binding different attributes of the scene. Indeed, the experience of being an undifferentiated observer may itself be an illusion, as after brain damage we can lose parts of our visual experience, such as our experience of colour [10] or motion [11]. Nevertheless, attributes of an object that change together appear to bind together, perhaps because perceptual synchrony implies a single common external cause.

As different attributes of an object are processed in different parts of the brain, and the information arrives there through different routes, it would be extraordinary if processing of all object attributes took the same time. Moutoussis and Zeki [1] recognised this and designed an experiment to measure differences in perceptual time, which they define as the time it takes for a percept to become established in a particular cortical area. They varied the colour of a set of dots on a computer monitor between red and green while at the same time changing the direction of motion between up and down (Figure 1). The relative phase of the two changes was varied from trial to trial, and subjects were asked to report the colour of the upward moving dots. They found that the likelihood of responding with the colour red, say, for downward movement was greatest when the colour changes lagged behind the motion direction changes by about 80 milliseconds.

The idea that the time we attribute to an event is tied to time at which the brain generates a representation of that event raises some thorny philosophical problems [12]. In the neural processing delay approach, which we call the

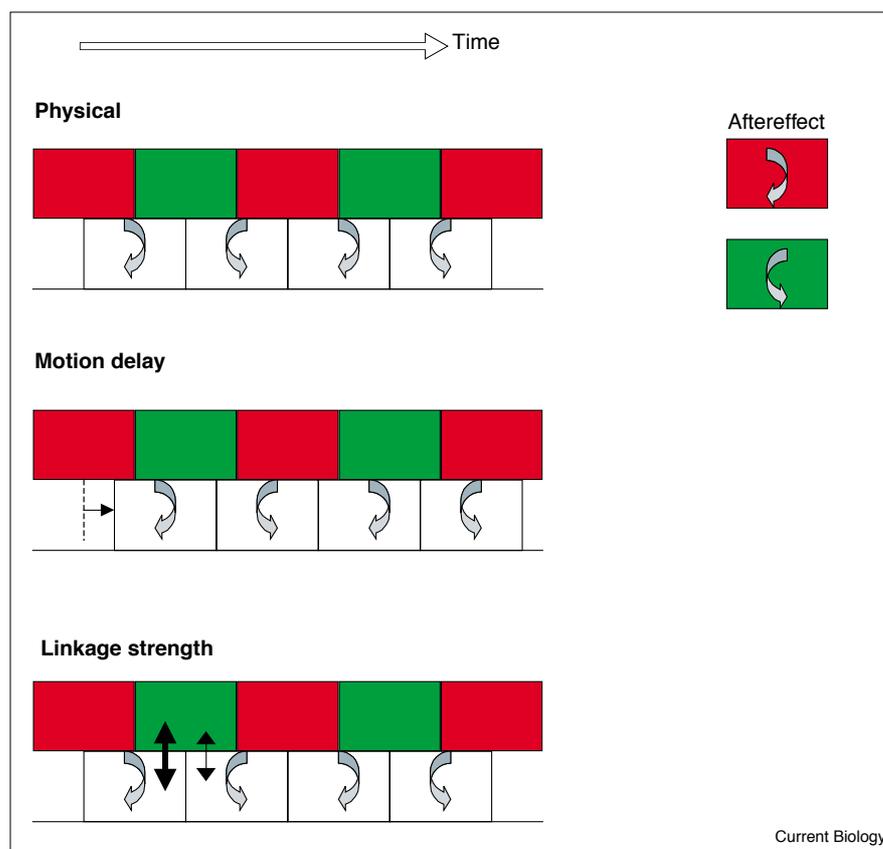
‘brain time’ theory, time is treated quite differently from other sensory attributes. Current vision theory is grounded on the idea that all visual information — for example, spatial pattern, colour, motion, depth, surface properties or object identity — is encoded in the activity of cortical neurons, the input to which is traceable through a network of neural connections to the sensory surface in the eye. The data for these processes is the spatio-temporal pattern of light on the retinae. Temporal perception may work in the same way: we may have specialised neural systems that encode the relative time of external events. We can call this alternative the ‘event time’ theory.

Brain time theories can take two forms. In the explicit form, relative time may be encoded by ‘metaneurons’ that are sensitive to the time course of neural processing in the brain. It is difficult to see the advantage of this approach. Problems of temporal perception are simply passed to higher level processes, in which distributed neural events remote from the input, and therefore subject to various kinds of temporal delay, are substituted for the events themselves.

The alternative, implicit form of brain time theory is more daunting, however. If our perception of the time of an event is coded implicitly, as the time at which a perceptual state of the brain is established — tantamount to the time at which we become aware of the contents of the event — then the medium of temporal sensory experience is no longer physical, as it is for the other five senses, it is conscious experience itself. In this theory, to make temporal judgments — for example whether colour changes

Figure 3

A motion delay could give rise to different strength of association between colour and motion, but another possibility is that there is a temporal asymmetry in the strength of the linkage. Either situation could generate contingent aftereffects for 90° or 270° physical phase shifts.



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before motion direction — we have to compare two micro-conscious experiences — occurring in different parts of the brain. There is a clear fundamental difficulty with this. The implicit brain time theory requires a perceptual mechanism that is outside the neural substrate. Intriguingly, this mechanism could provide a unique function for consciousness: the encoding of temporal relations in distributed brain areas, something that would be difficult, or perhaps impossible, to simulate in an artificial system. To propose this mechanism, however, would be to advocate breaking the link between neural activity and perceptual experience on which all current perceptual theory is based.

In the Moutoussis and Zeki [1] procedure, the evidence for errors in temporal binding comes from an observer's subjective reports of temporal order. These errors may reflect differences in neural processing time, or they may result from an imperfect specialist system for determining the temporal properties of events [13–14]. The new work of Arnold *et al.* [7] has provided further evidence for the neural processing time view (Figure 2). In this study, the magnitudes of so-called 'contingent aftereffects' were used as the dependent measure in place of temporal order judgements. After watching a slowly rotating stimulus, a

static stimulus appears to move in the opposite direction. This is a motion aftereffect. The aftereffect can be made contingent on colour by alternating between a clockwise red pattern and an anticlockwise green pattern. Subsequently, static green patterns appear to rotate clockwise and static red patterns appear to rotate anticlockwise.

Arnold *et al.* [7] systematically varied the relative phase of the motion and colour alternations and measured the magnitudes of the contingent aftereffects. The maximum contingent aftereffects arose for conditions in which the colour change and direction change were physically synchronised. However, the minimum aftereffects did not occur when the colour and motion changes were 90 degrees out of phase, as would be expected if colour and motion processing was in perfect temporal synchrony. When a range of relative phases were tested the average delay, as indicated by the centroid of the phase function, fell around 60–90 milliseconds away from the point of physical synchrony in the direction consistent with a delay in the neural processing of the motion change signal.

This result appears to provide convincing support for Moutoussis and Zeki's [1] finding that colour is processed

faster than motion. Arnold *et al.* [7] propose that temporal binding, as indicated by contingent aftereffects, reflects these neural processing delays. However, the physiological basis of contingent aftereffects is not well understood and caveats may be applied. There is an implicit assumption that contingent aftereffects will be greatest when the colour and motion changes are processed synchronously. More importantly, there is an assumption that when the colour and motion changes are 90° out of phase — that is, when for both clockwise and anticlockwise motion the colour is green for half the time and red for the other half — then the contingent effects precisely cancel each other out, so that the aftereffect function crosses zero at the 90° and 270° points. A relative temporal phase shift from this null point will strengthen the link between, say, green and clockwise. An asymmetry in contingent adaptation could have exactly the same effect without a phase shift however, if for example the motion direction, clockwise say, at the start of a colour segment, green say, is more effectively linked to the colour than the motion, anticlockwise, at the end of the colour segment (Figure 3). Interestingly, this explanation predicts maximum contingent aftereffects for synchronous patterns rather than for time-shifted patterns.

The colour contingent motion aftereffect may reflect a change in sensitivity of neurons responsive to both a particular colour and direction of motion, or an increase in mutual inhibition between neurons sensitive to colour and those sensitive to motion. Arnold *et al.* [7] do not make any specific suggestions in their paper about how the colour and motion information is combined in the generation of the contingent aftereffect. If it is necessary to combine information in a single cell or area, then this would be inconsistent with the picture of distributed asynchronous activation (implicit brain time) offered by Moutoussis and Zeki [1]. However, if there is no explicit neural connection, then it may be difficult to explain how the contingencies arise.

Temporal judgements, like judgements of spatial relationships, require us to interrogate our experience. We have to establish a perceptual routine to recover the information necessary for the task. But contingent aftereffects are automatic and appear sensitive to the temporal contingencies of neural processing. They therefore provide an important tool by which to investigate temporal processing in the visual system. However, the advantages of using an indirect measure of temporal processing need to be balanced against the disadvantages. We still need to establish whether these adaptation effects result from differences in processing time that directly influence our perception of the relative time of occurrence of external events.

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#### References

1. Moutoussis K, Zeki S: **Functional segregation and temporal hierarchy of the visual perceptive systems.** *Proc R Soc Lond [Biol]* 1997, **264**:1407-1414.
2. Moutoussis K, Zeki S: **A direct demonstration of perceptual asynchrony in vision.** *Proc R Soc Lond [Biol]* 1997, **264**:393-399.
3. Zeki S, Moutoussis K: **Temporal hierarchy of the visual perceptive systems in the Mondrian world.** *Proc R Soc Lond [Biol]* 1997, **264**:1415-1419.
4. Zeki S, Bartels A: **The asynchrony of consciousness.** *Proc R Soc Lond [Biol]* 1998, **265**:1583-1585.
5. Bartels A, Zeki S: **The theory of multistage integration in the visual brain.** *Proc R Soc Lond [Biol]* 1998, **265**:2327-2332.
6. Zeki S, Bartels A: **Toward a theory of visual consciousness.** *Conscious Cogn* 1999, **8**:225-259.
7. Arnold DH, Clifford CWG, Wenderoth P: **Asynchronous processing in vision: color leads motion.** *Curr Biol* 2001, **11**:596-600.
8. Zeki S: *A Vision of the Brain.* Oxford: Blackwells; 1993.
9. Wandell, BA: **Computational neuroimaging of human visual cortex.** *Annu Rev Neurosci* 1999, **22**:145-173.
10. Cowey A, Heywood, C: **Cerebral achromatopsia: colour blindness despite wavelength processing.** *Trends Cognit Sci* 1997, **1**:133-139.
11. Zihl J, Von Cramon D, Mai N: **Selective disturbance of movement vision after bilateral brain damage.** *Brain* 1983, **106**:313-340.
12. Dennett DC, Kinsbourne M: **Time and the observer: the where and when of consciousness in the brain.** *Behav Brain Sci* 1992, **15**:183-247.
13. Nishida S, Johnston A: **Perceptual asynchrony of colour and motion results from repetitive alternation.** *Invest Ophthalmol Vis Sci* 1999, **40**:S190.
14. Nishida S, Johnston A: **Dissociation of perceived temporal synchrony and response latency for changes in colour and motion.** *Invest Ophthalmol Vis Sci* 2000, **41**:S712.
15. Nishida S, Johnston A: **Perceptual delay for rapid direction alternations: a new account in terms of the dichotomy of first-order and second-order temporal changes.** *Perception* 2000, **29**(Suppl):27.