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Time, agency, and sensory feedback delays during action

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Until recently the plasticity of sensorimotor delay compensation mechanisms has received little scientific attention. In this paper, we review the work that is now taking place on this interesting topic. Imagine playing a computer game where the cursor lags behind the control movements. Can we behaviourally compensate for such delays with training? Do they eventually disappear from awareness? Recent results demonstrate that such temporal plasticity does indeed exist. It is constrained by the volition of participants' movements (agency), which introduces an asymmetry in timing: actions always precede their sensory consequences. As a result, the processing of sensory signals differs depending on whether they precede or follow an action. Additionally, the motor strategy used to compensate for the effects of sensory delays influences whether feedback delays are detected and hence whether temporal recalibration occurs.

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Introduction

During interaction with the environment, such as when catching a ball in flight, there are delays between the neural motor command to the muscles and the registration of the resulting sensory effects (Figure 1a). These delays amount on average to approximately 150 ms [1]. Neural delay compensation processes help us to experience sensory and motor events coherently in time and to interact with the world in a coordinated manner.

In this paper, we review recent experiments that studied the plasticity of delay compensation: if participants are trained in motor tasks with altered sensory feedback delays, such as a slowly responding computer game, can they compensate for the perturbing effect of sensory delays on sensorimotor control? Does training with altered feedback delays cause sensorimotor time perception to adapt? That is, do participants recalibrate the perceived simultaneity of kinaesthetically sensed movement signals and external sensory feedback to compensate for the presence of the training delay?

Temporal recalibration, like all sensorimotor adaptation, is driven by *error signals*, that is, discrepancies between the expected and the actual sensory outcome of an action. When registering a discrepancy, the brain needs to solve three non-trivial and interrelated problems to accurately recalibrate the perceptual and motor systems:

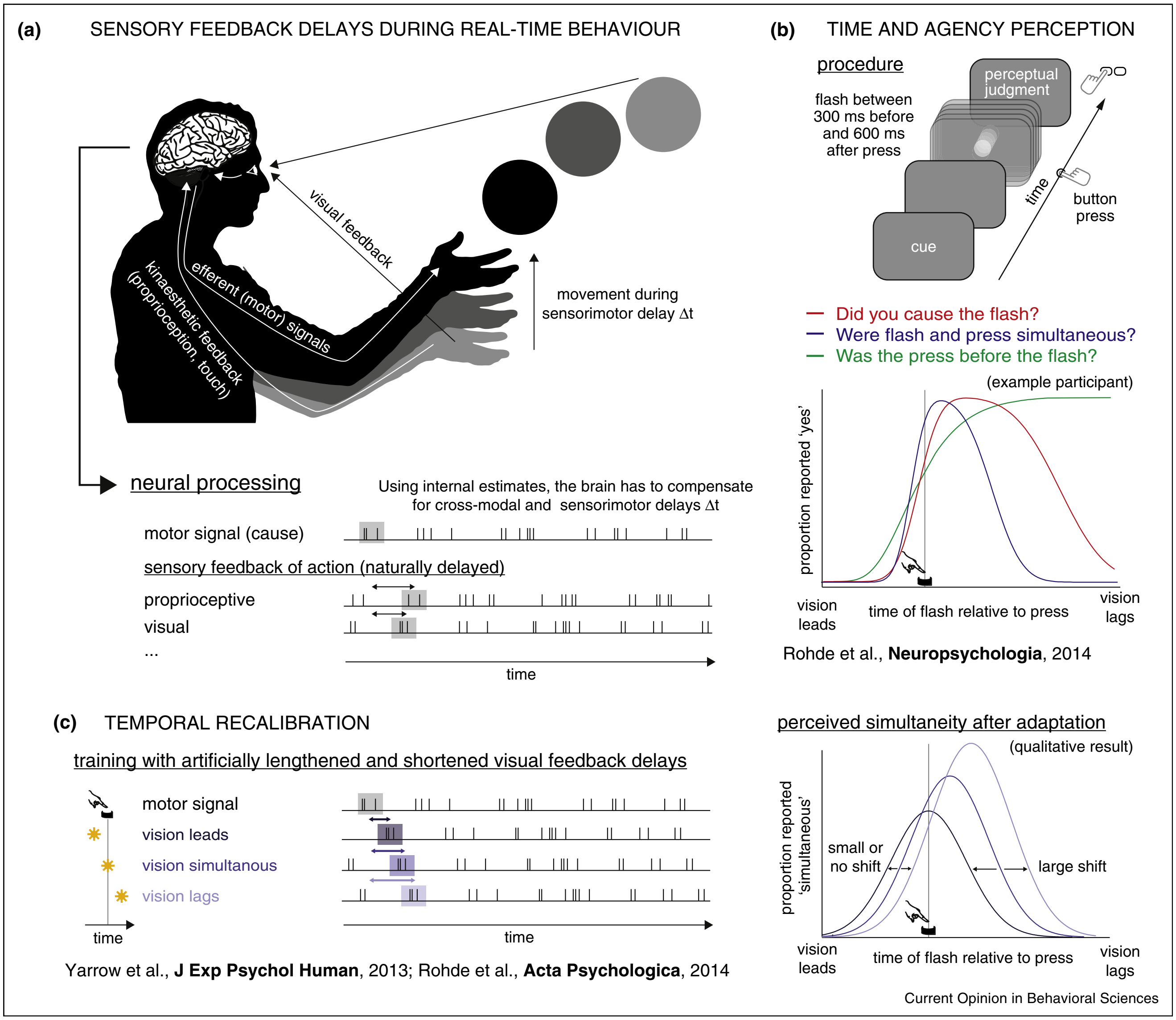
(1) *Correspondence detection*. Is the discrepancy a consequence of the agent's action, or caused by an external process?
(2) *Bias detection*. Is the error due to random variability or due to a systematic bias that can be eliminated by recalibration?
(3) *Error assignment*. What is the origin of a bias and which parameter(s) should be recalibrated?

We argue that sensorimotor feedback delays provide unique conditions for correspondence detection and error assignment. This is because action timing, and often action selection, are partially determined by the participant's volition, not by independently existing external factors. Temporal adaptation is thus different from spatial sensorimotor adaptation (e.g., to prismatic displacement of the visual field [2]) and from adaptation to crossmodal delays between passively sensed modalities (e.g., vision and audition [3]), where a participant's volition does not play this essential role.

Correspondence detection: the temporal asymmetry of agency

Physically, effects follow their causes in time. A sensory event that occurs before a voluntary and self-initiated action event cannot be its causal consequence (cf. Box 1). Perceptually, this manifests as an asymmetrical time window of agency [4•]: when judging whether an action caused a visual flash (correspondence detection), participants tolerate stimuli that lag the action up to around 500 ms, which is a perceptible delay, but vehemently deny causing stimuli that occur even shortly before the action (Figure 1b).

Figure 1



Sensory feedback delays in perception and behavior. **(a)** The human brain has to compensate for naturally occurring delays (Δt) between movement signals and sensory feedback signals when interacting in real-time with the environment (predictive motor control) and in the perception of visual and motor simultaneity. **(b)** Time and agency judgments about sensory stimuli presented around the time of action as a function of sensorimotor delay. Visual stimuli presented before a voluntary button press are perceived differently than stimuli presented afterwards [4•]. **(c)** When training participants in conditions that either shorten (dark blue) or lengthen (light blue) sensory feedback delays, the time window of perceived simultaneity is adaptively recalibrated in an asymmetrical manner (growing and shrinking on the side of lagging visual stimuli) [5•,6•].

This temporal asymmetry of perceived agency is reflected in asymmetrical distortions of sensorimotor time perception. The time window of perceived simultaneity of actions and sensory events is larger on the side of lagging stimuli than on the side of leading stimuli [4•,5•,6•] (see Figure 1b). This is probably due to *intentional* [7] or *causal binding* [8],[1] that is, a subjective compression of the time interval between an intentional action and its assumed sensory effect [7]. The reverse temporal pattern, that is, binding for leading sensory events, occurs if participants react to a go-signal: the temporally leading go-signal is temporally bound to the subsequent action that it triggers [10].

These temporal constraints on the inference of agency can be modulated by contextual factors, such as beliefs about delayed causality [11] or the presence of additional sensory cues [4•,12]. For instance, participants judging

[1] See [9] for a comparative study of intentional binding (involving action) and the weaker case of causal binding (not involving action).