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Perception: A Motion After-Effect for Voluntary Actions

After viewing directional motion for a period of time, we experience a motion after-effect in which a subsequent stationary object appears to move in the opposite direction. A recent study demonstrates a novel motion after-effect that depends on the movement of the hand.

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That we use sensory information to guide our actions is clear to all. What is less obvious is how this happens. The study of the relationship between perception and action is closely related to the question of how space is coded in the nervous system. In other words, the coding of sensory space, or ‘frame of reference’, is generally different from the coding of motor space. Most previous research has focused on how the visual space is converted to motor space, for example in reaching for objects in the environment [1]. A psychophysical study reported in this issue of *Current Biology* [2] provides evidence for a relation in the reverse direction, by showing that voluntary hand movement can also influence the coding of visual space. Matsumiya and Shioiri [2] studied the motion after-effect, an illusion of visual motion resulting from adaptation to a moving stimulus [3]. The authors provide evidence that the motion after-effect, traditionally considered to have a retinotopic frame of reference [4], can be anchored to the hand — but only if

the hand is both seen and voluntarily moved.

Frames of Reference for Perception and Action

A frame of reference is defined as a set of axes that describes the location of an object in relation to another point. To perform accurate goal-directed actions, the representation of the location of a sensory stimulus on the receptive surface needs to be transformed into a representation that is appropriate for a specific effector (Figure 1). For example, to reach a visual target with the hand, visual input in retinotopic coordinates needs to be converted to an arm-centered frame of reference. Only after this transformation can the motor system compute the differences between current and desired arm positions, and compute the appropriate motor command to reach for the target [1].

How and where could such transformation occur? Neurons in the posterior parietal cortex (PPC) transform sensory signals that are used to guide actions into a common frame of reference for perception and action [1,5]. Furthermore, there is evidence

that neurons in the macaque PPC and premotor cortex (PMC) respond to sensory input near the body, in any of several different modalities. Importantly, the receptive fields of these neurons are centered on motor effectors [6,7]. Because the neurons encode the position of stimuli in the surrounding environment with respect to the body, so-called ‘peripersonal space’, it has been proposed that they play a role in guiding actions towards objects within reaching distance [8].

Frames of Reference of the Motion After-Effect

In a typical motion after-effect experiment, participants are not required to perform any action, nor is the vision of their body experimentally manipulated. Previous investigations on the frame of reference of the motion after-effect have largely been confined to retinotopic and head-centered accounts. Many studies have shown that the motion after-effect is strictly retinotopic [4]: in other words, it occurs when adaptor and test stimuli fall on the same region of the retina. Recent evidence suggests that the motion after-effect may also occur when adaptor and test gratings are not retinotopically overlapping, but share the same coordinates with respect to the head [9].

Matsumiya and Shioiri [2] investigated for the first time the motion after-effect during visible active movement of the hand. They report a novel motion after-effect that is anchored to one’s own hand, when the

hand is both visible and actively moved. Participants adapted to a grating drifting in one direction near their hand, while moving the hand in a circular motion and in full view. After adaptation, participants stopped moving their hand, and made a first saccade towards a visual target; the target was then shifted leftwards, and participants made a second saccade towards it. A test grating was then displayed in counterphase flicker with variable phase shift, and the task was to indicate the direction in which the test grating appeared to drift. Motion after-effect was measured as the phase shift necessary to null the perceived drifting direction of the test grating.

There were four conditions: adaptation and test gratings presented in overlapping locations in both hand-centered and retinal coordinates (#1: 'Hand and Retina'); adaptation and test gratings presented in overlapping locations in either hand-centered (#2: 'Hand') or retinal coordinates (#3: 'Retina') only; adaptation and test gratings presented at different locations in either hand-centered or retinal coordinates (#4: 'Non-matched'). Matsumiya and Shioiri [2] found a larger motion after-effect in the 'Hand' condition compared to the 'Non-matched' condition. Moreover, the motion after-effects in the 'Hand', 'Retina', and 'Hand and Retina' had comparable magnitude. The hand-centered motion after-effect occurred even when adaptation and test-gratings were presented at separate locations in spatiotopic (head-centered) coordinates, demonstrating that it was anchored on the actively moved body part.

Importantly, the hand-centered motion after-effect was specific for *seeing one's own hand during active movement*: it disappeared when the participants could not see their hand which was actively moved, saw an object moving at its place, viewed a stationary hand, or viewed their hand being passively moved by a robot.

Effector-Centered Visual Motion Analysis

The new work of Matsumiya and Shioiri [2] suggests the existence of a visual motion system which is not only centered on a motor effector, but is also effector-view dependent and active-movement dependent. The properties of such a system go far beyond our current knowledge about

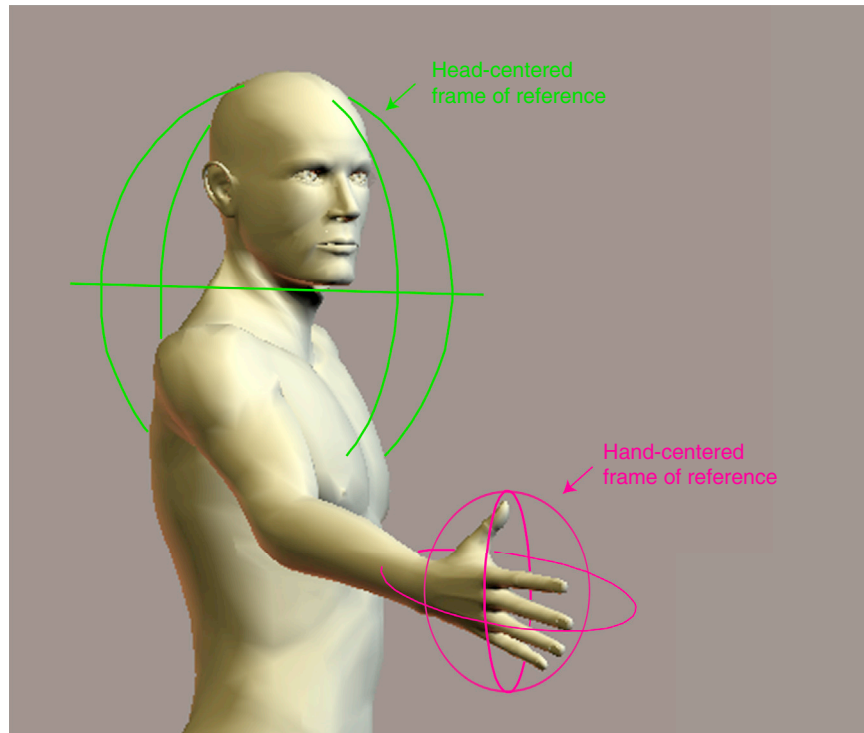


Figure 1. The motor space.

Motor effectors are coded in frames of reference centered on that body part. For example, head movements are coded in head-centered frames of reference (green), and hand movements are coded in hand-centered coordinates (pink).

visual motion analysis. The new results are somewhat in line with recent findings that the spatiotemporal processing of visual motion for quick hand control is effector-specific: namely, it is different from that for quick eye control [10]. This suggests that visual analysis may be dynamically tailored to specific motor effectors, and raises the question of the neural correlates of effector-centered visual motion processing.

The neural basis of the retinotopic motion after-effect is fairly well established. The motion after-effect is produced by the imbalance in the relative responses of neural populations with different direction preferences in the middle temporal complex (area MT), [11]. The spatial organization in MT is debated [12]: there is considerable evidence for retinotopic mapping [13], but other studies reported additional spatiotopic, or mixed representations depending on attention [14]. Could MT alone generate the hand-centered motion after-effect? This seems unlikely, given that the effect also requires a visible voluntary movement.

Neural Correlates of the Motion After-Effect for Voluntary Movements
Matsumiya and Shioiri's findings [2] indicate that voluntary movements can structure the visual space, generating perceptual representations in effector-centered frames of reference. Voluntary movements are generally characterized by the feeling that we move *our own* body [15]. To investigate whether the sense of ownership over the seen and moved hand contributes to the motion after-effect, Matsumiya and Shioiri [2] induced an illusion of ownership of a virtual hand (namely, the 'rubber-hand' illusion). They demonstrated that the hand-centered motion after-effect occurred only when participants sensed that the seen and moved hand was part of their body.

Neuroimaging studies on the rubber-hand illusion have proposed that activity in PMC reflects the sense of ownership of a limb [16]. Given that PMC is also involved in the preparation of voluntary movements [17], and responds to polymodal motion [18], Matsumiya and Shioiri [2] speculate that neurons in PMC are the most likely neural candidates for the hand-centered motion after-effect.

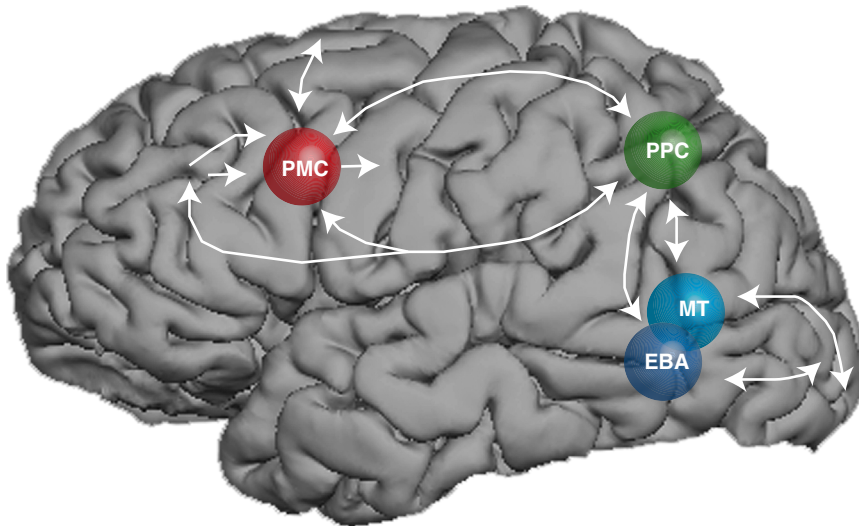


Figure 2. Proposed neural networks underlying the motion after-effect for voluntary movements.

The motion after-effect for voluntary movements may arise from the dynamic interplay of neural networks for visual motion analysis and motor control. Area MT and the extrastriate body area (EBA) analyse visual motion of objects and bodies. Both regions are reciprocally connected to areas in the posterior parietal cortex (PPC), which compute spatial transformations from retinotopic frames of reference to effector-centered frames of reference. PPC sends and receives information from frontal networks for motor control, which involve the premotor cortex (PMC).

Although this view is tempting, complex sensorimotor behavior is rarely generated by individual brain centers, but is more often the orchestrated product of large neural networks. Furthermore, the authors make the strong assumption that the sense of ownership is ‘coded’ in PMC, which is, however, controversial [15].

We suggest an alternative view (Figure 2). The hand-centered motion after-effect for visible movements points at the interdependency between visual motion circuits for objects (targeting MT) and bodies (involving the extrastriate body area, EBA) [19], and frontal networks for motor control. PPC is likely to be the key communication node between these networks [1], possibly tuning MT activity in a frame of reference anchored to the body [20]. Future studies may shed light on the neural mechanisms that allow voluntary actions to structure the visual space.

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Development: The Maternal–Zygotic Transition Revisited

The handover from maternal to zygotic control has to be carefully orchestrated. In most animal embryos, maternal products drive early embryogenesis, and the genome of the zygote is only switched on later. However, in the nematode *Ascaris* the zygotic genome is never silent, and the maternal products are rapidly eliminated.

Mark Blaxter

In 1883, Édouard van Beneden published “*Recherches sur la*

maturation de l’oeuf, la fécondation et la division cellulaire” [1]. This beautifully illustrated monograph describes in exquisite detail the