Visuo-manual Coordination

►Eye-Hand Coordination

Visuomotor

Definition

Refers to transformations between vision and motor processes involving the eyes and or the limbs.

►Eye-Hand Coordination

Visuomotor Integration

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Synonyms

Visuomotor transformation; Visuomotor interaction

Definition

Visuomotor integration is the coordination of neuronal activity between visual-related and motor-related parts of the brain in order to influence behavior and perception.

Characteristics

Vision and Movement

Vision guides movement, and movement affects vision. To facilitate the coordination between vision and movement, reciprocal interactions are needed between brain areas involved in visual and motor processing. The use of visual information to influence movement processing, and movement information to influence visual processing, is termed visuomotor integration.

For primates, vision is the primary sense. It drives behaviors as diverse as looking around a scene and moving through the world. Visual information arrives from the ►retina, is interpreted by a network of ►visual processing areas in the brain (Fig. 1, yellow arrows), and is sent to subcortical areas that cause movement generation (red arrows). In turn, movements may influence visual input, and so information about actions is fed back to visual processing areas to close the loop (Fig. 1, grey arrows).

Visuomotor integration varies in its details depending on the behavioral context and the effector used, e.g., eye or hand. There are four general aspects of visuomotor integration, however. First, visuomotor integration is relatively slow. Vision is useful for planning movements but sluggish for online control, and the time from visual input to motor output is surprisingly long and variable. Second, visuomotor integration is spatially organized. The retina is a finely grained two-dimensional map, and central brain regions recapitulate this map. Third, visuomotor integration is adaptive. The relationship between visual input and motor output is continuously monitored and adjusted as necessary. Fourth, visuomotor integration is bidirectional. Not only are visual signals transformed to motor commands, but motor commands are fed back to aid visual processing. Here we review these four components of visuomotor integration.

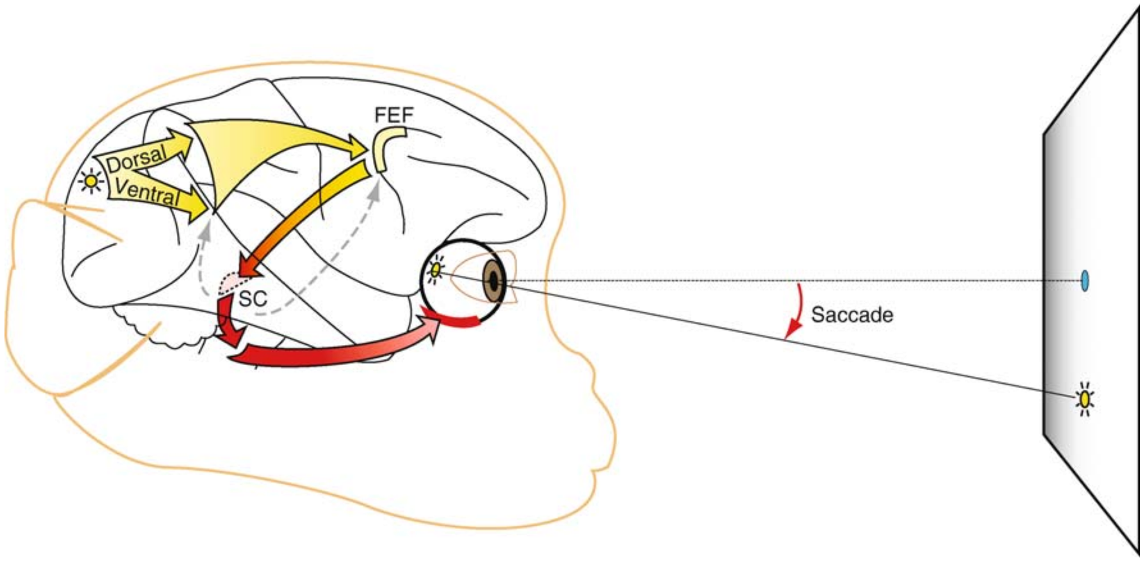
Visuomotor Integration is Relatively Slow

A good way to begin analyzing a system is to consider its input. Characteristics of the input limit the possible ways that the system may produce an output. Visual information is the input to visuomotor transformations, and vision is one of our slower senses. Vision helps to initiate movements but may be too slow for the real-time control of movements.

After visual information is transduced by ►photoreceptors, approximately 70 ms elapses before it reaches central areas for visuomotor integration. Added to this afferent lag are further delays related to planning. The final reaction times of visuomotor acts are typically around 200 ms. These afferent lags and reaction times are about 50 ms longer than analogous delays for auditory inputs and 20 ms longer than for skin receptor inputs.

At the output of visuomotor transformation, many movements take less than 70 ms to complete. Hence the movements terminate before visual feedback can provide information about movement progress. Brief movements, therefore, can be triggered but not continuously controlled by visual signals. Such movements must be ►ballistic (open-loop) or controlled by non-visual feedback.

An example of a short-duration movement that is triggered but not controlled by vision is the ►*saccade*, a rapid eye movement that relocates the fovea to a new part of the scene. To minimize time in flight (when vision is blurred on the retina), and maximize time during fixation (when vision is optimal), saccades have high velocity and short duration. For most naturally occurring saccades (<15° amplitude), the duration is



Visuomotor Integration. Figure 1 Neuronal circuits for visuomotor integration in the primate brain. Illustrated as an example circuit is the core network for ►saccade generation. While a monkey foveates one stimulus (*blue dot*), another suddenly appears (*yellow dot*). The goal is to make a saccade to the new stimulus. An image of the yellow stimulus is projected onto the retina and encoded in ►primary visual cortex (*far left*; the pathway from retina to visual cortex is omitted for clarity). The location of the visual stimulus is processed by a ►dorsal pathway, the identity of the stimulus by a ►ventral pathway, and the processed information is sent to visuomotor areas such as the ►FEF (*yellow arrows*). From there, signals are sent to the ►SC and other brainstem areas to cause eye muscle contraction (*red arrows*). Feedback information about saccades is sent to cerebral cortex to close the loop (*grey arrows*). Modified from [1].

less than 50 ms. Such movements, therefore, are too fast for visual feedback. Even for large, long duration saccades, visual feedback is blurred by the fast eye motion. The low-level saccade generating circuitry (in the ►pons and ►midbrain) controls saccadic progress not with visual feedback, but with internal estimates of the eye's instantaneous state [2].

Certain eye movements, such as ►smooth pursuit, are slower and may use vision for control. The function of smooth pursuit is to keep the eyes foveated on a moving object such as a bird in flight. Smooth pursuit can persist for several seconds, so visual feedback is able to influence the ongoing movement. Continual visual input is compared with predictions of the input, and if there is a mismatch, pursuit velocity is adjusted.

As note above, visual sluggishness has two main components: initial, afferent lag and subsequent planning-related lags. The planning stage seems to begin in ►parietal and frontal cortex, after basic visual scene analyses are performed by ►occipital cortex. Cortex is only a few synapses above the oculomotor muscles. It is intriguing, therefore, that the time from the start of parietal/frontal cortex activation to the start of the movement is long (~100 ms) and variable. The delay is used for cortical computations that select the next movement as a function of past, present, and predicted future visual inputs [3,4].

Visuomotor Integration is Spatially Organized

Visual information reaches about one third of the primate ►cerebral cortex and much of the brainstem. Many of these brain areas are laid out in a visually ordered ►topographic manner. We focus on two of the areas as examples of the spatial aspects of visuomotor integration. These are the ►frontal eye field (FEF) in frontal cortex, and the intermediate layers of the ►superior colliculus (SC), in the midbrain (Fig. 1). Both the FEF and intermediate SC contain neurons that are active for incoming visual stimuli as well as outgoing eye movement commands; moreover, electrical stimulation of each area evokes saccades and inactivation of each area impairs saccades. Thus, the FEF and the SC are implicated in using visual information to guide the execution of saccades. Visually guided skeletal movements, such as moving one's hand, depend on comparable areas of the cortex and brainstem, as well as the spinal cord.

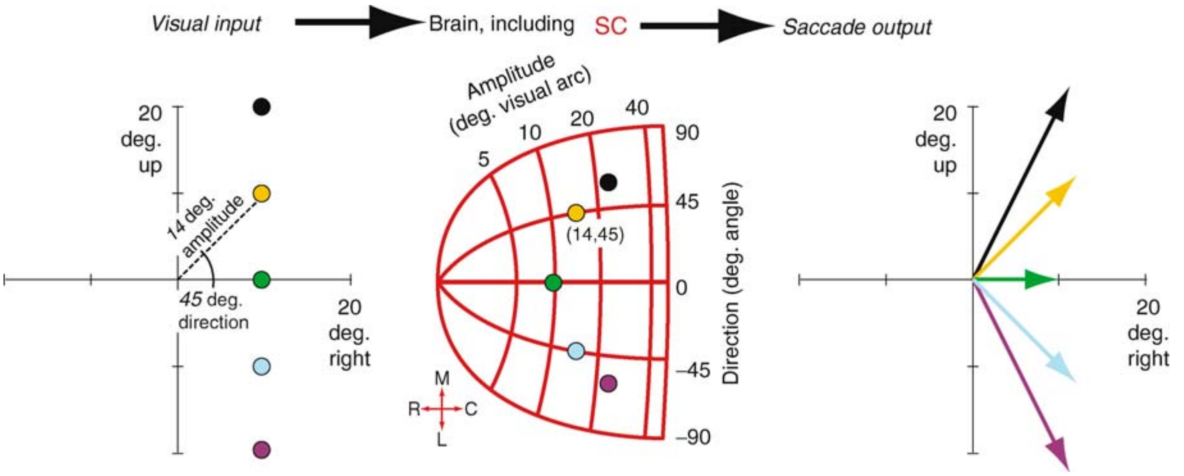
Spatial orderliness begins in the two-dimensional sheet of the retina. Visual stimuli produce a pattern of activity on the retina that reflects the layout of stimuli in the real world. The pattern is recapitulated throughout the visual system with high fidelity. This maintenance of spatial relationships is due to connections that form repeated topographies. For the purpose of visual analysis, ►topographic maps facilitate form discrimination and other spatial evaluations. For the purpose of visuomotor integration, the maps offer an efficient link between the ▶visual field and the motor workspace.

The FEF and SC contain neurons that are active for visual input (so-called visual neurons), saccade generation (movement neurons), or both (visuomovement neurons) [5,6]. Neurons with visual responses fire for stimuli falling within a certain retinal zone called the receptive field. Neurons with saccade-related activity fire for saccades having a certain range of vectors (amplitudes and directions) that delimits the movement field. Visual and movement neurons are arrayed together such that neighboring neurons have similar receptive fields and movement fields. For visuomovement neurons, which have both a receptive field and a movement field, the two fields are coincident. Across the FEF and SC, receptive fields and movement fields vary systematically. In an elegant fashion, therefore, evolution and development have interlinked the visual and motor maps. This spatial organization plays a vital role in transforming visual input to eye movement output.

To see why the overlap of visual and motor maps is beneficial, consider a simple example. Imagine you are looking straight ahead and see something in the upper-right portion of your peripheral vision, for example a yellow dot (Fig. 2, left). The dot will activate a discrete portion of your retinas and then a corresponding location on the FEF and SC visual maps (for the SC map, the location is shown with a yellow dot in Fig. 2, middle). Each visual map is spatially integrated with a coincident movement map, and therefore locations on each map encode not only a visual stimulus but also the vector of saccade needed to foveate the stimulus (Fig. 2, right, yellow arrow). All locations in contralateral space are represented in each FEF and SC map (other colored dots and arrows in Fig. 2).

Although visuomotor maps in FEF and SC are similar, there are some notable differences between them. Pure visual-related neurons are common in the FEF but rare in the SC intermediate layers. Overall, FEF neurons seem to play more of a role in representing visual targets for saccades, while SC neurons seem more related to saccadic dynamics such as instantaneous motor error and velocity. Also, the SC map is more finely elaborated in terms of movement vectors. In both the SC and FEF, saccadic amplitude is well organized, but in the SC saccadic direction is laid out explicitly too, in a mapping orthogonal to amplitude (Fig. 2). In the FEF there may be some directional organization, but it seems patchy [5].

The differences between the FEF and SC maps suggest that the former is more visual and the latter more motor in nature. This is not to say, however, that visuomotor transformations proceed in a leap from visual FEF to motor SC, or between any two structures. The differences between FEF and SC are a matter of degree, and visuomotor transformations are best characterized as gradual [7]. Neuronal activity slowly loses its dependence on vision and gains a tight relation to movement as it proceeds from area to area. Below the SC, spatial codes of saccadic vectors are transformed into temporal codes that



Visuomotor Integration. Figure 2 Visuomotor transformation using a ▶topographic map. *Left*: Visual stimuli (*dots*) in the right visual field. The *yellow dot* appears ~14° from the fovea at an angle of 45° up from horizontal. *Middle*: Stimuli in the right visual field are encoded on the left SC visuomotor map, shown schematically. The rostral (R) to caudal (C) dimension represents increasing amplitudes of distance from the fovea. The lateral (L) to medial (M) dimension represents increasing angles relative to horizontal. The *yellow dot* in the visual field is encoded by neurons at site (14, 45) on the SC map. Other visual stimuli are encoded by corresponding sites. *Right*: The neuronal output of the SC map causes saccades. Neurons driven by the *yellow dot* cause a saccade of 14° amplitude angled 45° up from horizontal (*yellow arrow*). Neurons elsewhere on the map generate other saccadic vectors (*other arrows*). Modified from [6].

precisely coordinate the contractions of oculomotor muscles.

In the skeletal motor system, movement topographies are present as well. However, the spatial relations between visual input and skeletal movements (e.g., arm movements) are more complex and variable than those between vision and eye movements. The ultimate control region for skeletal motor execution seems to be ▶primary motor cortex, which contains neurons with visual (and other sensory) inputs arranged in a body map. How the spatiotemporal transformation occurs from this map to the alpha-▶motoneurons of the spinal cord is the focus of much physiology and modeling.

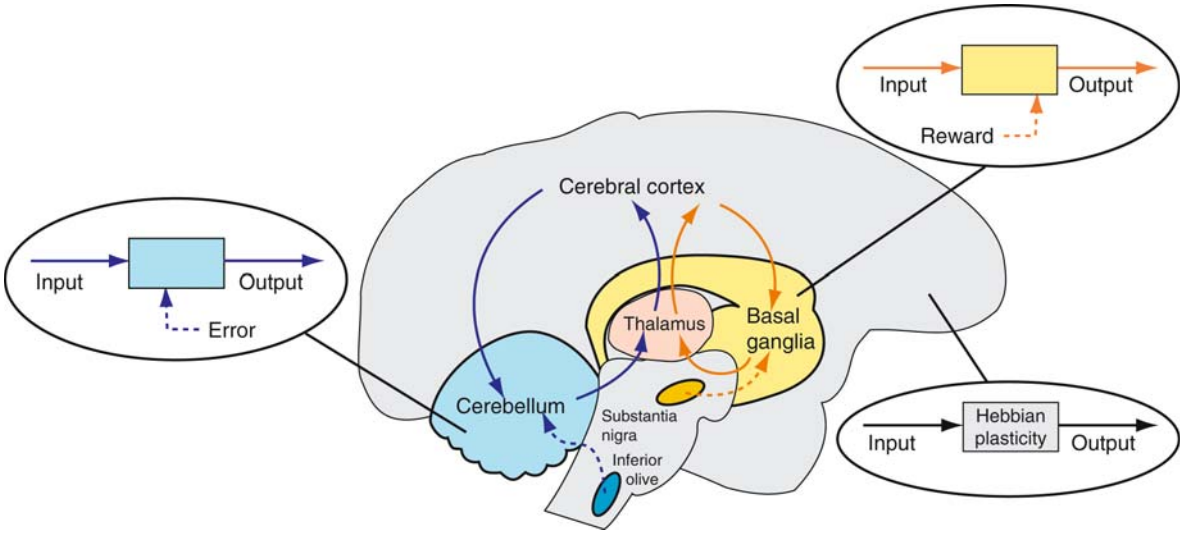
Visuomotor Integration is Adaptive

Visuomotor integration must be able to change as our body and surroundings change. From infancy to adulthood the relation of the retinas to the rest of the body is altered extensively, and yet visually guided movements must stay accurate. Even in adults, injury can alter visual input, motor output, or the relation between the two. The environment changes too, requiring behaviors to adapt accordingly.

▶Adaptation can be quick, as shown by donning prism glasses; within only a few dozen trials, eye and reaching movements are re-calibrated to adjust for the altered visual input. Once a visuomotor relation is adapted, the new behavior can persist for life.

While steady-state visuomotor integration mostly involves the cerebral cortex, brainstem, and spinal cord, plasticity in visuomotor integration relies on two extensive subcortical networks: the ▶cerebellum and the ▶basal ganglia [8,9]. The cerebellum (Fig. 3, left) is most critical for short-term adaptation as in the prism glasses example. Error signals that represent unexpected differences between visual input and motor output reach the cerebellum via ▶climbing fibers from the ▶inferior olive. These error signals have a strong, long-lasting effect on cerebellar activity. This altered cerebellar activity is relayed through ▶thalamus to modify visuomotor transformations in the cerebral cortex.

The basal ganglia play a broader role in adaptation. Rather than micro-managing movements on a millisecond time scale as the cerebellum, the basal ganglia seem to help select which movement is appropriate given the context of the situation. This context may change to require a different motor response for the same visual input. Context-dependent adaptation in basal ganglia depends on occurrence of reward (Fig. 3, upper right). Reward is reported by dopaminergic neurons in the substantia nigra and other brainstem regions that feed back to the input nodes of the basal ganglia. The feedback alters basal ganglia activity, and as with the cerebellum, the altered neuronal activity is relayed by thalamus to influence visuomotor transformation in the cerebral cortex.



Visuomotor Integration. Figure 3 Circuits for visuomotor adaptation. A silhouette of the monkey brain is shown with the critical subcortical networks for adaptation superimposed. *Left*: The cerebellar loop receives visual information from cerebral cortex and other areas and relays the information back to cortex through ▶thalamus. The feedback to cortex is modified, however, by error signals provided by the inferior olive. *Upper right*: The basal ganglia loop is similar, but its signals are modified by reward, for example from the ▶substantia nigra (pars compacta). *Lower right*: Many neurons in the cerebral cortex also have the capacity to adapt through intrinsic, Hebbian, processes, so that input-output (visual-saccade) relationships may change with ▶long-term potentiation or depression. Modified from [8].

Finally, it should be noted that many neurons have an intrinsic capacity for input-output plasticity. Any neuron may be involved in adaptation as long as its action potential output can be modified for a given pattern of afferent input, for example via ►Hebbian synaptic plasticity. Some adaptation mechanisms may be resident in cerebral cortex, therefore, and independent of basal ganglia and cerebellum (Fig. 3, lower right).

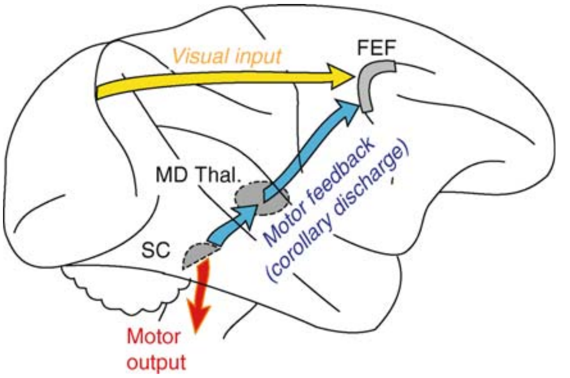
Visuomotor Integration is Bidirectional

Every movement that we make causes spurious changes to our sensory input. A major problem for the brain is to disregard the sensory artifacts of self-movement while maintaining sensitivity to sensory changes caused by external objects. One way that the brain solves this problem is by copying the outgoing motor command and sending this copy back to visual areas to provide information about the upcoming movement. Such copies of motor commands are called ►corollary discharge or ►efference copy [1].

Just as saccades have proven a good model for studying visual-to-motor processes, they have been equally important for understanding motor-to-visual processes. Saccades permit rapid relocation of the fovea, but an attendant visual artifact is the sudden displacement of the entire scene across the retina. If we were to perceive the visual world as actually detected by the retinas, we would see the world jumping from place to place every time we make a saccade. Yet we enjoy a percept of visual stability. To complicate things further, some objects in the visual scene move on their own, and the brain must distinguish those movements from the saccade-induced visual artifacts. Corollary discharge is crucial for the joint processes of stabilizing our visual percept across saccades and distinguishing real object motion from saccade-induced motion.

Where does the corollary discharge originate, and where does it travel to influence vision? One corollary discharge pathway ascends from the SC to the FEF via a thalamic relay node (Fig. 4). When the SC issues a movement command to lower saccade-generating circuits, it sends a corollary discharge of the command to the FEF (blue arrows). The corollary discharge encodes information about saccadic timing, size, and direction, allowing the FEF to prepare for the imminent eye movement and its visual consequences.

Within the FEF, corollary discharge interacts with visual input arriving from earlier visual areas (Fig. 4, yellow arrow). One result is that some visual neurons suddenly sample a new part of the visual field just before the eyes begin to move [10]. Such shifting receptive fields allow neurons to analyze the same region of absolute visual space (in ►world-centered coordinates) before and after each saccade. Hence this mechanism may help to stabilize our percept of the visual scene across saccades.



Visuomotor Integration. Figure 4 Example circuit for motor-to-visual feedback. As in Fig. 1, visual input is sent to the FEF (*yellow arrow*) and motor output descends from the SC (*red arrow*). In addition, a copy of the motor output ascends as feedback through mediodorsal thalamus (MD Thal.) to the FEF (*blue arrow*). Such feedback is known as corollary discharge. As discussed in the text, corollary discharge interacts with visual input at single FEF neurons to cause shifting receptive fields. The general function of corollary discharge is to help the visual system interpret whether changes in visual input represent trivial artifacts of self-movement or real changes in the external environment. Modified from [1].

Smooth pursuit is another example of a behavior that requires an ongoing, internal estimate of movement progress. As noted above, visual feedback is used by the smooth pursuit system to monitor accuracy and control the movement in real time. But the actual control process requires the visual input to be compared with a prediction, and that prediction requires an internal estimate of the ongoing eye movement. This estimate could be provided by corollary discharge or by ►proprioception, i.e., the sense of muscle position.

Summary

Visuomotor integration is the coordination of sensation with action. Distributed cortical-subcortical circuits transform visual input to motor output in a manner that is spatially precise but relatively slow. The circuits, and their attendant visuomotor processes, change as needed. Because movements influence visual input, corollary discharge of movements closes the loop. The basic principles of visuomotor integration as established for eye movements are likely to hold for skeletomotor movements as well.

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Visuomotor Space

► Visual Space Representation for Reaching

Visuomotor Transformation

Definition

Refers to transformations between vision and motor processes involving the eyes and or the limbs.

► Visuomotor Integration

Visuospatial Attention

Definition

Visuospatial attention refers to mechanisms by which a particular spatial location in the visual field is selected for further processing. The processing of stimuli appearing at the attended spatial location will be enhanced, while stimuli appearing at neighboring regions will be suppressed. Visuospatial attention can be directed either overtly or covertly. During overt attention, attention is linked to the eye gaze direction. During covert attention, the oculomotor and attention systems operate independently, allowing attention to be deployed throughout the visual field while the eye gaze remains fixed. Visuospatial attention can be deployed prior to stimulus onset, biasing processing in favor of any upcoming stimuli presented at the attended location.

► Visual Attention

Visuospatial Disorientation

Definition

Some brain-damaged patients can identify objects, but have problems in visually locating them or their distance. These patients also cannot look at named objects or cannot navigate correctly so as to avoid bumping into them. The damage is typically in the occipital-parietal area on both sides. Visuo-spatial disorientation occasionally concurs with ►simultanagnosia, both of which are components of ►Balint's syndrome. Focal parietal lesions may lead to impairment of the perception of horizontal and vertical axes, of length and distance estimation, orientation discrimination and position matching.

► Visual Neuropsychology

Visuospatial Hemineglect

Definition

► Visual Neuropsychology

Vitalism

Definition

The idea, associated with Pasteur in the nineteenth century and with Driesch in the early twentieth century,