
Visual sensitivity is markedly reduced during an eye movement. Peri-saccadic vision is also characterized by a mislocalization of the briefly presented stimulus closer to the saccadic target. These features are commonly viewed as obligatory elements of peri-saccadic vision. However, practice improves performance in many perceptual tasks performed at threshold conditions. We wondered if this could also be the case with peri-saccadic perception. To test this, we used a paradigm in which subjects reported the orientation (or location) of an ellipse briefly presented during a saccade. Practice on peri-saccadic orientation discrimination led to long-lasting gains in that task but did not alter the classical mislocalization of the visual stimulus. Shape discrimination gains were largely generalized to other untrained conditions when the same stimuli were used (discrimination during a saccade in the opposite direction or at a different stimulus location than previously trained). However, performance dropped to baseline level when participants shifted to a novel Vernier discrimination task under identical saccade conditions. Furthermore, practice on the location task did not induce better stimulus localization or discrimination. These results suggest that the limited visual information available during a saccade may be better used with practice, possibly by focusing attention on the specific target features or a better readout of the available information. Saccadic mislocalization, by contrast, is robust and resistant to top-down modulations, suggesting that it involves an automatic process triggered by the upcoming execution of a saccade (e.g., an efference copy signal).


What happens to the representation of a moving stimulus when it is no longer present and its motion direction has to be maintained in working memory (WM)? Is the initial, sensorial representation maintained during the delay period or is there another representation, at a higher level of abstraction? It is also feasible that multiple representations may co-exist in WM, manifesting different facets of sensory and more abstract features. To that end, we investigated the mnemonic representation of motion direction in a series of three psychophysical experiments, using a delayed motion-discrimination task (relative clockwise?counter-clockwise judgment). First, we show that a change in the dots’ contrast polarity does not hamper performance. Next, we demonstrate that performance is unaffected by relocation of the Test stimulus in either retinotopic or spatiotopic coordinate frames. Finally, we show that an arrow-shaped cue presented during the delay interval between the Sample and Test stimulus, strongly biases performance toward the direction of the arrow, although the cue itself is non-informative (it has no predictive value of the correct answer). These results indicate that the representation of motion direction in WM could be independent of the physical features of the stimulus (polarity or position) and has non-sensorial abstract qualities. It is plausible that an abstract mnemonic trace might be activated alongside a more basic, analog representation of the stimulus. We speculate that the specific sensitivity of the mnemonic representation to the arrow-shaped symbol may stem from the long term learned association between direction and the hour in the clock.
McKytan, A, Ben-Zion I, Doron R, Zohary E. 2015. The Limits of Shape Recognition following Late Emergence from Blindness. Current biology : CB. Abstract

Visual object recognition develops during the first years of life [1]. But what if one is deprived of vision during early post-natal development? Shape information is extracted using both low-level cues (e.g., intensity- or color-based contours) and more complex algorithms that are largely based on inference assumptions (e.g., illumination is from above, objects are often partially occluded) [2]. Previous studies, testing visual acuity using a 2D shape-identification task (Lea symbols), indicate that contour-based shape recognition can improve with visual experience, even after years of visual deprivation from birth [3]. We hypothesized that this may generalize to other low-level cues (shape, size, and color), but not to mid-level functions (e.g., 3D shape from shading) that might require prior visual knowledge. To that end, we studied a unique group of subjects in Ethiopia that suffered from an early manifestation of dense bilateral cataracts and were surgically treated only years later. Our results suggest that the newly sighted rapidly acquire the ability to recognize an odd element within an array, on the basis of color, size, or shape differences. However, they are generally unable to find the odd shape on the basis of illusory contours, shading, or occlusion relationships. Little recovery of these mid-level functions is seen within 1 year post-operation. We find that visual performance using low-level cues is relatively robust to prolonged deprivation from birth. However, the use of pictorial depth cues to infer 3D structure from the 2D retinal image is highly susceptible to early and prolonged visual deprivation.


Parietal cortex is often implicated in visual processing of actions. Action understanding is essentially abstract, specific to the type or goal of action, but greatly independent of variations in the perceived position of the action. If certain parietal regions are involved in action understanding, then we expect them to show these generalization and selectivity properties. However, additional functions of parietal cortex, such as self-action control, may impose other demands by requiring an accurate representation of the location of graspable objects. Therefore, the dimensions along which responses are modulated may indicate the functional role of specific parietal regions. Here, we studied the degree of position invariance and hand/object specificity during viewing of tool-grasping actions. To that end, we characterize the information available about location, hand, and tool identity in the patterns of fMRI activation in various cortical areas: early visual cortex, posterior intraparietal sulcus, anterior superior parietal lobule, and the ventral object-specific lateral occipital complex. Our results suggest a gradient within the human dorsal stream: along the posterior-anterior axis, position information is gradually lost, whereas hand and tool identity information is enhanced. This may reflect a gradual transformation of visual input from an initial retinotopic representation in early visual areas to an abstract, position-invariant representation of viewed action in anterior parietal cortex.


Regions in the occipitotemporal cortex (OTC) show clear selectivity to static images of human body parts,
and upper limbs in particular, with respect to other object categories. Such selectivity was previously attributed to shape aspects, which presumably vary across categories. Alternatively, it has been proposed that functional selectivity for upper limbs is driven by processing of their distinctive motion features. In the present study we show that selectivity to static upper-limb images and motion processing go hand in hand. Using resting-state and task-based functional MRI, we demonstrate that OTC voxels showing greater preference to static images of arms and hands also show stronger functional connectivity with motion coding regions within the human middle temporal complex (hMT+), but not with shape-selective midtier areas, such as hV4 or LO-1, suggesting a tight link between upper-limb selectivity and motion processing. To test this directly, we created a set of natural arm-movement videos where kinematic patterns were parametrically manipulated, while keeping shape information constant. Using multivariate pattern analysis, we show that the degree of (dis)similarity in arm-velocity profiles across the video set predicts, to a significant extent, the degree of (dis)similarity in multivoxel activation patterns in both upper-limb-selective OTC regions and the hMT+. Together, these results suggest that the functional specificity of upper-limb-selective regions may be partially determined by their involvement in the processing of upper-limb dynamics. We propose that the selectivity to static upper-limb images in the OTC may be a result of experience-dependent association between shape elements, which characterize upper limbs, and upper-limb-specific motion patterns.


2012


Accurately perceiving the velocity of an object during smooth pursuit is a complex challenge: although the object is moving in the world, it is almost still on the retina. Yet we can perceive the veridical motion of a visual stimulus in such conditions, suggesting a nonretinal representation of the motion vector. To explore this issue, we studied the frames of representation of the motion vector by evoking the well known motion aftereffect during smooth-pursuit eye movements (SPEM). In the retinotopic configuration, due to an accompanying smooth pursuit, a stationary adapting random-dot stimulus was actually moving on the retina. Motion adaptation could therefore only result from motion in retinal coordinates. In contrast, in the spatiotopic configuration, the adapting stimulus moved on the screen but was practically stationary on the retina due to a matched SPEM. Hence, adaptation here would suggest a representation of the motion vector in spatiotopic coordinates. We found that exposure to spatiotopic motion led to significant adaptation. Moreover, the degree of adaptation in that condition was greater than the adaptation induced by viewing a random-dot stimulus that moved only on the retina. Finally, pursuit of the same target, without a random-dot array background, yielded no adaptation. Thus, in our experimental conditions, adaptation is not induced by the SPEM per se. Our results suggest that motion computation is likely to occur in parallel in two distinct representations: a low-level, retinal-motion dependent mechanism and a high-level representation, in which the veridical motion is computed through integration of information from other

We apply functional magnetic resonance imaging and multivariate analysis methods to study the coordinate frame in which saccades are represented in the human cortex. Subjects performed a memory-guided saccade task in which equal-amplitude eye movements were executed from several starting points to various directions. Response patterns during the memory period for same-vector saccades were correlated in the frontal eye fields and the intraparietal sulcus (IPS), indicating a retinotopic representation. Interestingly, response patterns in the middle aspect of the IPS were also correlated for saccades made to the same destination point, even when their movement vector was different. Thus, this region also contains information about saccade destination in (at least) a head-centered coordinate frame. This finding may explain behavioral and neuropsychological studies demonstrating that eye movements are also anchored to an egocentric or an allocentric representation of space rather than strictly to the retinal visual input and that parietal cortex is involved in maintaining these representations of space.


Viewed object-oriented actions elicit widespread fMRI activation in the dorsal and ventral visual pathways. This activation is typically stronger in the hemisphere contralateral to the visual field in which action is seen. However, since in previous studies participants kept fixation at the same screen position throughout the scan, it was impossible to infer if the viewed actions are represented in retina-based coordinates or in a more elaborated coordinate system. Here, participants changed their gaze between experimental conditions, such that some conditions shared the same retinotopic coordinates (but differed in their screen position), while other pairs of conditions shared the opposite trait. The degree of similarity between the patterns of activation elicited by the various conditions was assessed using multivoxel pattern analysis methods. Regions of interest, showing robust overall activation, included the intraparietal sulcus (IPS) and the occipitotemporal cortex. In these areas, the correlation between activation patterns for conditions sharing the same retinotopic coordinates was significantly higher than that of those having different retinotopic coordinates. In contrast, the correlations between activation patterns for conditions with the same spatiotopic coordinates were not significantly greater than for non-spatiotopic conditions. These results suggest that viewed object-oriented actions are likely to be maintained in retinotopic-framed coordinates.


The human primary motor cortex (M1) is robustly activated during visually guided hand movements. M1 multivoxel patterns of functional MRI activation are more correlated during repeated hand movements to the same targets than to greatly differing ones, and therefore potentially contain information about movement direction. It is unclear, however, whether direction specificity is due to the motor command, as implicitly assumed, or to the visual aspects of the task, such as the target location and the direction of the cursor's trajectory. To disambiguate the visual and motor components, different visual-to-motor transformations were applied during an fMRI scan, in which participants made visually guided hand
movements in various directions. The first run was the "baseline" (i.e., visual and motor mappings were matched); in the second run ("rotation"), the cursor movement was rotated by 45° with respect to the joystick movement. As expected, positive correlations were seen between the M1 multivoxel patterns evoked by the baseline run and by the rotation run, when the two movements were matched in their movement direction but the visual aspects differed. Importantly, similar correlations were observed when the visual elements were matched but the direction of hand movement differed. This indicates that M1 is sensitive to both motor and visual components of the task. However, repeated observation of the cursor movement without concurrent joystick control did not elicit significant activation in M1 or any correlated patterns of activation. Thus, visual aspects of movement are encoded in M1 only when they are coupled with motor consequences.

2010

In monkeys, neurons in the hand representation of the primary motor cortex (M1) are often tuned to the direction of hand movement, and there is evidence that these neurons are clustered according to their "preferred" direction of movement. However, this organizational principle has yet to be demonstrated in M1 of humans. We conducted a functional magnetic resonance imaging (fMRI) study in which participants used a joystick to move a cursor from a central origin to one of five equidistant targets. The fMRI signal of individual voxels was sensitive to the directional aspects of the reaching task and manifested direction-specific adaptation. Furthermore, the correlation between multivoxel patterns of responses for different movement directions depended on the angular distance between them. We conclude that M1 neurons are likely to be organized in clusters according to their preferred direction, since only such a coarse-grained representation can lead to directional selectivity of voxels, encompassing millions of neurons. A simple model that estimates cluster size suggests that the diameter of these clusters is on the order of a few hundred micrometers.

Inhibition of return (IOR), a performance decrement for stimuli appearing at recently cued locations, occurs when the target and cue share the same screen position. This is in contrast to cue-based attention facilitation effects that were recently suggested to be mapped in a retinotopic reference frame, the prevailing representation throughout early visual processing stages. Here, we investigate the dynamics of IOR in both reference frames, using a modified cued-location saccadic reaction time task with an intervening saccade between cue and target presentation. Thus, on different trials, the target was present either at the same retinotopic location as the cue, or at the same screen position (e.g., spatiotopic location). IOR was primarily found for targets appearing at the same spatiotopic position as the initial cue, when the cue and target were presented at the same hemifield. This suggests that there is restricted information transfer of cue position across the two hemispheres. Moreover, the effect was maximal when the target was presented 10 ms after the intervening saccade ended and was attenuated in longer delays. In our case, therefore, the representation of previously attended locations (as revealed by IOR) is not remapped slowly after the execution of a saccade. Rather, either a retinotopic representation is remapped rapidly, adjacent to the end of the saccade (using a prospective motor command), or the positions of the cue and target are encoded in a spatiotopic reference frame, regardless of eye position. Spatial attention
can therefore be allocated to target positions defined in extraretinal coordinates.


(PURPOSE) Recent studies show evidence of multisensory representation in the functionally normal visual cortex, but this idea remains controversial. Occipital cortex activation is often claimed to be a reflection of mental visual imagery processes triggered by other modalities. However, if the occipital cortex is genuinely active during touch, this might be the basis for the massive cross-modal plasticity observed in the congenitally blind. (METHODS) To address these issues, we used fMRI to compare patterns of activation evoked by a tactile object recognition (TOR) task (right or left hand) in 8 sighted and 8 congenitally blind subjects, with several other control tasks. (RESULTS) TOR robustly activated object selective regions in the lateral occipital complex (LOC/LOtv) in the blind (similar to the patterns of activation found in the sighted), indicating that object identification per se (i.e. in the absence of visual imagery) is sufficient to evoke responses in the LOC/LOtv. Importantly, there was negligible occipital activation for hand movements (imitating object palpations) in the occipital cortex, in both groups. Moreover, in both groups, TOR activation in the LOC/LOtv was bilateral, regardless of the palpating hand (similar to the lack of strong visual field preference in the LOC/LOtv for viewed objects). Finally, the most prominent enhancement in TOR activation in the congenitally blind (compared to their sighted peers) was found in the posterior occipital cortex. (CONCLUSIONS) These findings suggest that visual imagery is not an obligatory condition for object activation in visual cortex. It also demonstrates the massive plasticity in visual cortex of the blind for tactile object recognition that involves both the ventral and dorsal occipital areas, probably to support the high demand for this function in the blind.


Large-scale topographic representations of the body have long been established in the somatosensory and motor cortices. Using functional imaging, we identified a topographically organized body part map within the occipitotemporal cortex (OTC), with distinct clusters of voxels showing clear preference for different visually presented body parts. This representation was consistent both across hemispheres and participants. Using converging methods, the preference for specific body parts was demonstrated to be robust and did not merely reflect shape differences between the categories. Finally, execution of (unseen) movements with different body parts resulted in a limited topographic representation of the limbs and trunk, which partially overlapped with the visual body part map. This motor-driven activation in the OTC could not be explained solely by visual or motor imagery of the body parts. This suggests that visual and motor-related information converge within the OTC in a body part specific manner.


Present theories of visual recognition emphasize the role of interactive processing across populations of neurons within a given network, but the nature of these interactions remains unresolved. In particular, data describing the sufficiency of feedforward algorithms for conscious vision and studies revealing the functional relevance of feedback connections to the striate cortex seem to offer contradictory accounts of visual information processing. TMS is a good method to experimentally address this issue, given its excellent temporal resolution and its capacity to establish causal relations between brain function and
behavior. We studied 20 healthy volunteers in a visual recognition task. Subjects were briefly presented with images of animals (birds or mammals) in natural scenes and were asked to indicate the animal category. MRI-guided stereotaxic single TMS pulses were used to transiently disrupt striate cortex function at different times after image onset (SOA). Visual recognition was significantly impaired when TMS was applied over the occipital pole at SOAs of 100 and 220 msec. The first interval has consistently been described in previous TMS studies and is explained as the interruption of the feedforward volley of activity. Given the late latency and discrete nature of the second peak, we hypothesize that it represents the disruption of a feedback projection to V1, probably from other areas in the visual network. These results provide causal evidence for the necessity of recurrent interactive processing, through feedforward and feedback connections, in visual recognition of natural complex images.

2009

Pertzov, Y, Avidan G, Zohary E. 2009 Accumulation of visual information across multiple fixations [33]. Journal of Vision. 9:2.1-12. Abstract [34] Humans often redirect their gaze to the same objects within a scene, even without being consciously aware of it. Here, we investigated what type of visual information is accumulated across recurrent fixations on the same object. On each trial, subjects viewed an array comprised of several objects and were subsequently asked to report on various visual aspects of a randomly chosen target object from that array. Memory performance decreased as more fixations were directed to other objects, following the last fixation on the target object (i.e. post-target fixations). In contrast, performance was enhanced with increasing number of fixations on the target object. However, since the number of post-target fixations and the number of target fixations are usually anti-correlated, memory gain may simply reflect fewer post-target fixations, rather than true accumulation of information. To rule this out, we conducted a second experiment, in which the stimulus disappeared immediately after performing a predefined number of target fixations. Additional fixations on the target object resulted in improved memory performance even under these strict conditions. We conclude that, under the present conditions, various aspects of memory monotonically improve with repeated sampling of the same object.

Pertzov, Y, Zohary E, Avidan G. 2009 Implicitly perceived objects attract gaze during later free viewing [35]. Journal of Vision. 9:6.1-12. Abstract [36] Everyday life frequently requires searching for objects in the visual scene. Visual search is typically accompanied by a series of eye movements. In an effort to explain subjects’ scanning patterns, models of visual search propose that a template of the target is used, to guide gaze (and attention) to locations which exhibit "suspicious" similarity to this template. We show here that the scanning patterns are also clearly influenced by implicit (unrecognized) cues: A backward masked object, presented before the scene display, automatically attracts gaze to its corresponding location in the following inspected image. Interestingly, subliminally observed words describing objects do not have the same effect. This demonstrates that visual search can be unconsciously guided by activated target representations at the perceptual level, but it is much less affected by implicit information at the semantic level. Implications on search models are discussed.

{McKayton}, A, Pertzov Y, Zohary E. 2009 Pattern matching is assessed in retinotopic coordinates [37]. Journal of Vision. 9:19.1-10. Abstract [38] We typically examine scenes by performing multiple saccades to different objects of interest within the image. Therefore, an extra-retinotopic representation, invariant to the changes in the retinal image caused
by eye movements, might be useful for high-level visual processing. We investigate here, using a matching
task, whether the representation of complex natural images is retinotopic or screen-based. Subjects
observed two simultaneously presented images, made a saccadic eye movement to a new fixation point,
and viewed a third image. Their task was to judge whether the third image was identical to one of the two
earlier images or different. Identical images could appear either in the same retinotopic position, in the
same screen position, or in totally different locations. Performance was best when the identical images
appeared in the same retinotopic position and worst when they appeared in the opposite hemifield.
Counter to commonplace intuition, no advantage was conferred from presenting the identical images
in the same screen position. This, together with performance sensitivity for image translation of a few degrees,
suggests that image matching, which can often be judged without overall recognition of the scene, is
mostly determined by neuronal activity in earlier brain areas containing a strictly retinotopic representation
and small receptive fields.

2008

Shmuelof, L, Zohary E. 2008 Mirror-image representation of action in the anterior parietal cortex [39].
Nature Neuroscience. 11:1267?1269. Abstract [40]
Mimicking hand actions made by someone facing us (that is, allocentric viewpoint) is typically performed
with the opposite hand. Using functional magnetic resonance imaging {(fMRI)}, we found a similar mirror-
image representation of others' actions in the human anterior parietal cortex. Viewing egocentric-based
actions elicited greater {fMRI} activation in the contralateral hemisphere (as in, self action), whereas
observation of action seen from an allocentric viewpoint generated greater activation in the ipsilateral
hemisphere. This mirror-like mapping occurs without active imitation, providing further evidence for an
automatic action-simulation system in the parietal cortex.

Saccades are ubiquitous in natural vision. One way to generate a coherent representation of a scene
across saccades is to produce an extra-retinal coordinate frame (such as a head-based representation).
We investigate this issue by behavioral means: Participants learned to detect a {3D-pop-out} target in a
fixed position. Next, target was relocated in one coordinate frame while maintaining it fixed in the others.
Performance was severely affected only when the change in target position occurred in a retinotopic
coordinate frame. This further suggests that perceptual learning occurs in retinotopic regions having
receptive fields restricted within a hemifield.

Stark, A, Zohary E. 2008 Parietal mapping of visuomotor transformations during human tool
During daily life, we reach and grasp objects located in a variety of positions in our visual-field. Where is
the information regarding the visual (position) and motor (acting-hand) aspects integrated in the brain? To
address this question, a functional magnetic resonance imaging experiment was conducted, in which 10
right-handed subjects used their right or left hand to grasp 3-dimensional tools, located to the right or left of
a central fixation point. The posterior part of the intraparietal sulcus {(IPS)}, the putative human homolog of
{caudal-IPS}, was found to be primarily involved in representing the visual location of the tools, whereas
more anterior regions, the human homologs of medial intraparietal area and anterior intraparietal, primarily
encoded the identity of the contralateral acting-hand. Quantitative analysis revealed 2 opposite visual and
motor gradients along the posterior-anterior axis within the {IPS:} although the importance of the visual-
field gradually diminished, the weight of the acting-hand became increasingly greater. Moreover, direct
evidence for visuomotor interaction was found in all 3 (IPS) subregions, but not in occipital or frontal regions. These findings support the hypothesis that the human (IPS) is comprised of subregions that have different properties, and that it is engaged in visuomotor transformations necessary for visually guided prehension.

2007


Recent neuroimaging and transcranial magnetic stimulation studies indicate that the occipital cortex of congenitally blind humans is functionally relevant for nonvisual tasks. There are suggestions that the underlying cortical reorganization is restricted by a critical period. These results were based on comparison between early and late blind groups, thereby facing the problem of great variability among individuals within each group. Using functional magnetic resonance imaging, we studied bilingual congenitally blind individuals during use of 2 languages: one acquired early (Hebrew), the other later in life (English, at approximately 10 years). The subjects listened to chimeric words consisting of superimposed Hebrew and English nouns. They were instructed to either covertly generate a verb to the heard noun or repeat the noun, in either Hebrew or English. Lateralized activation during verb generation (vs. repeat) was found in classical language areas, in congruence with previous studies in sighted subjects. Critically, in our study, the blind participants typically also had robust left lateralized occipital differential activation during verb generation (vs. repeat), in both languages. This suggests that the critical period for plasticity persists beyond 10 years or that the visual cortex of the blind might be engaged in abstract levels of language processing, common to the 2 languages.
The Jerusalem Brain Sciences Building will provide a state-of-the-art research and teaching facility for the Edmond and Lily Safra Center for Brain Sciences.

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