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Linking form and motion in the primate brain

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Understanding dynamic events entails the integration of information about form and motion that is crucial for fast and successful interactions in complex environments. A striking example of our sensitivity to dynamic information is our ability to recognize animate figures by the way they move and infer motion from still images. Accumulating evidence for form and motion interactions contrasts with the traditional dissociation between shape and motion-related processes in the ventral and dorsal visual pathways. By combining findings from physiology and brain imaging it can be demonstrated that the primate brain converts information about spatiotemporal sequences into meaningful actions through interactions between early and higher visual areas processing form and motion and frontal-parietal circuits involved in the understanding of actions.

Introduction

Successful interactions in the complex and dynamic environments we inhabit requires that the visual system integrates information about the form and motion of objects and actors into dynamic perceptual events. Traditionally, motion and form processing have been attributed to anatomically and functionally separable neural pathways in the primate brain [1]. For instance, an extrastriate visual area in the medial temporal monkey cortex (MT/V5) and its human homologue in the ascending limb of the inferior temporal sulcus (hMT+/V5) are known as prototypical motion areas that mediate the analysis and perception of visual motion [2,3]. Areas in the occipitotemporal cortex (V4 and inferior temporal cortex), by contrast, are thought to be specialized for the analysis of shape properties [4,5] and serve as prototypical form areas.

Despite the recent advances in elucidating the neural mechanisms that mediate motion and form perception, less is known about the possible interactions of these mechanisms that might underlie the unified perception of dynamic objects. Clear evidence that form and motion processing interact comes from psychophysical studies. For example, motion facilitates the detection of shapes embedded in cluttered backgrounds [6], the invariant representations of object views that fall within the path of the object motion [7] and the discrimination and identification of faces [8]. By contrast, form influences the perception of motion. For example, the biomechanical structure of the human body

constrains the perception of motion paths [9], and local orientation signals (e.g. lines trailing behind a moving object that are oriented in the direction of the motion of the object) influence the perception of motion direction [10,11] and resolve motion direction ambiguity [12].

Recent advances in brain imaging provide us with the unique opportunity to study cortical circuits involved in form and motion perception and their interactions in both the human and the monkey brain using the same methods and paradigms. Here, we combine recent evidence about the neural mechanisms that mediate form and motion interactions at the level of large-scale populations and cortical circuits, as measured by brain imaging, and at the single neuron level, as recorded in monkey electrophysiological experiments. First, we discuss how motion signals aid form perception. Second, we investigate the converse: how form signals aid motion perception. Taken together, physiological and brain imaging studies demonstrate that the interactions between the visual form and motion pathways are much more extensive than commonly thought. These interactions are crucial for the perception of dynamic forms and guide our actions and interactions in complex environments.

Form from motion

The perception of biological motion is a striking demonstration of the role of motion in the perception of animate form. Johansson [13] demonstrated the ability of humans to recognize human actions from the mere movement of small points of light attached to the joints of an otherwise invisible human actor. The uncanny ability of humans to extract complex attributes such as gender or emotional state from these simple motion patterns suggests both the ecological relevance and the likelihood that specialized mechanisms operate to construct this biological form percept from motion [14].

Inanimate 3D structure, typically much simpler than animate form, is also readily extracted from 2D motion patterns. This process, commonly referred to as structure from motion (SFM), is most often investigated with rotating cylinders. In these displays, a collection of dots moves as if they are pasted on the transparent surface of a rotating cylinder. This results in a characteristic distribution of motion vectors (large horizontal speeds in the center of the display, slow speeds at the edges) that both humans and monkeys [15] readily interpret as a rotating cylinder.

The neural network for form from motion

Animate form from motion

Neurophysiological and imaging studies in monkeys have shown that neural populations in the superior temporal polysensory area (STP) are sensitive to biological motion [16–18]. Human brain imaging studies have identified the posterior superior temporal sulcus (STS) as the primary area involved in the perception of biological motion in humans. In particular, this region has been shown to be activated more strongly by point-light animations depicting human actions than by the same animations presented upside down, scrambled sequences of dots moving in sinusoidal trajectories typical of biological movements, dots translating or defining rotating 3D shapes [19–22]. hMT+/V5 has also been shown to respond more strongly to intact than scrambled sequences of biological motion but these activations seem to relate to the complex motion content rather than the biological properties of the stimulus [22]. Interestingly, a region in the human temporal cortex known to be involved in the analysis of the static human body form (the extrastriate body area) is also shown to be selectively activated by biological motion displays [23]. However, recent studies report that activations for biological motion in ventral stream areas [22,24,25] relate primarily to the form properties defining the human figure.

Inanimate form from motion

Although there is an extensive literature investigating structure from motion, a strong case for the involvement of an early motion area in the analysis of 3D form has been made in a relatively small number of studies. Specifically, neurons in MT are highly suitable for the analysis of structure from motion; not only are they exquisitely motion sensitive, but they also encode information on depth through their binocular disparity dependence [2]. This could provide the basis for a mechanism that translates 2D motion vectors into 3D structural information [26]. To determine whether area MT in the macaque is indeed involved in the percept of structure from motion, researchers have used stimuli defined by dots moving coherently but at different speeds, such that they evoke the percept of a rotating cylinder. Whereas the percept of motion and structure in this stimulus is vivid, the percept of motion direction is ambiguous, without disparity information. That is, when the same motion pattern is presented to both eyes, the underlying 3D structure can either be a leftward or a rightward rotating cylinder. By providing different images (with appropriate disparity) to the two eyes, the ambiguity can be resolved. If a neuron is involved in the SFM percept, one would expect its neural response to be more similar to the response to the unambiguously leftward rotating cylinder in the trials in which the animal reports perceiving a leftward rotating cylinder, and vice versa. Studies in MT confirm this prediction [27–29] but the same stimuli used in V1 did not show any significant association between behavioral choice and neural response. These findings suggest that the computation of structure from motion starts as early as in MT, but not in V1. However, this does not exclude the involvement of later areas. For example, neurons in the anterior STP can detect whether or not a motion pattern corresponds to a coherent global cylinder [30].

Recent imaging studies have shown activation for coherent motion [31] and structure from motion in a network of cortical regions in both the ventral lateral occipital sulcus and the dorsal stream {V3A, hMT+/V5 and intraparietal sulcus [IPS]} in humans [32–34] and monkeys [3]. hMT+/V5 corresponds to the macaque MT/V5 but also to several of its satellites [e.g. the medial superior temporal (MST) and fundus superior temporal (FST) regions] (Box 1). Activations in the human motion complex, and in particular in the ventral part corresponding to the FST region, reflect selective processing of 3D shape from motion [32,33,35,36] and the 3-D structure of static objects [35]. Further recent imaging studies in both humans and monkeys show responses in ventral and dorsal parietal regions along the IPS that might relate to the visuomotor control of actions [37–39] (e.g. human–object or tool interactions). Interestingly, these representations of 3D shape from motion are more extensive in the human than the monkey IPS [3,40,41], potentially because of the more extensive tool use in humans compared with monkeys.

Motion from form

A striking example of our sensitivity to dynamic information is our ability to infer motion from still images depicted in paintings, photographs or cartoons. We readily recognize whether an animal, person or object within a photograph was moving or standing still at the moment the photograph was taken. Photographers, painters, sculptors and cartoonists can successfully convey motion information, even

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Box 1. Monkey and human cortical homologies in motion processing

fMRI studies using the same paradigms and stimuli in both humans and monkeys provide a powerful method for identifying homologies across species; that is, they enable us to define anatomical and functional similarities between cortical regions in the human and the monkey brain. Despite advances in the recording and analysis of brain imaging data, comparing the functional anatomy between humans and monkeys is far from trivial. The 30 million years of evolution that separate the two species have led to large-scale differences in the anatomy (cortical expansion and convolution) and connectivity of different cortical regions that might also be reflected in diverging functional specialization. For example, striate and extrastriate visual areas lie on the medial surface along the calcarine sulcus in the human brain, whereas in the monkey brain they are located on the lateral surface. MT/V5 is located in the STS in monkeys, whereas the area with the most similar functional properties lies in the inferior temporal sulcus in humans. Surface-based warping methods [40,72], in combination with functional activation maps acquired across species using equivalent paradigms, enable us to uncover such functional homologies in the face of anatomical differences. Interestingly, this approach has revealed a comparatively larger expansion of the parietal than the ventral cortical surface in the human brain, suggesting a potential expansion of action- and motion-related functions in humans. Consistent with this proposal, motion processing is more prominent in the human than monkey IPS. In particular, ventral and dorsal regions in the human, but not the monkey, IPS are activated by structure from motion [33,41]. By contrast, homologies across species have been reported in anterior and posterior (lateral intraparietal and caudal intraparietal) IPS regions, suggesting that the most pronounced differences across species are in the middle part of the IPS, which has been implicated in 3D motion perception.

though no real motion is present in their work. Cartoonists, for instance, use the inanimate form cue of speed lines to suggest motion in an effective manner. Motion in art is often implied by animate form cues. In the case of human figures, these cues include body posture, articulation of arms and legs, and the overall imbalance of the body. This type of animate implied motion shows how form can lead to a 'sense' of motion, and the study of implied motion aims to uncover how the brain uses form cues to generate the percept of motion.

Several behavioral studies provide evidence that motion perception is influenced by form and speak to the functional relevance of form and motion interactions in natural environments (Box 2). For example, both human [10,11] and non-human primates [42] have been shown to use elementary form cues such as oriented lines to improve or even generate the percept of motion. Further, form information can be used to disambiguate motion perception. When a static figure that implies motion is presented in front of a counterphase grating with an ambiguous direction of motion, the perceived direction of motion is consistently in the direction opposite to the implied motion direction [43]. Finally, spatial memory is influenced by form cues that imply motion, as shown by studies of representational momentum. When presented with a static frame of a person in motion, observers mentally extrapolate the spatial position of the person in the direction of its implied motion [44].

The neural network for motion from form
Animate implied motion
Neurophysiological studies in monkeys show a strong selectivity for animate implied motion in single neurons of the anterior STS (STSa) regions [45,46]. These STSa cells are specialized for the perception of bodily actions and postures [45–49]. Cell selectivity in this cortical area is diverse and complex. Of the cells that respond to static

images of human figures, ~60% are sensitive to the degree of articulation shown by the human. About half of the cells sensitive to images of human figures prefer implied motion, whereas the other half of the cells prefer standing or sitting images [45]. These findings suggest that STSa processes high-level form information that is related to motion perception. However, whether the interactions between implied and real motion take place in STSa or reflect feedback from frontoparietal areas engaged in the execution and observation of actions remains an open question.

In the human, functional magnetic resonance imaging (fMRI) studies have shown that pictures with implied motion evoke strong responses in hMT+/V5, as in the Enigma visual illusion [50], or a snapshot of an athlete running [51] or a cup falling off a shelf [52]. Such activations are observed not only when observers passively view images that imply motion, but also, importantly, when an orthogonal task is employed (e.g. repetition detection [51]) to ensure that observers attend similarly to
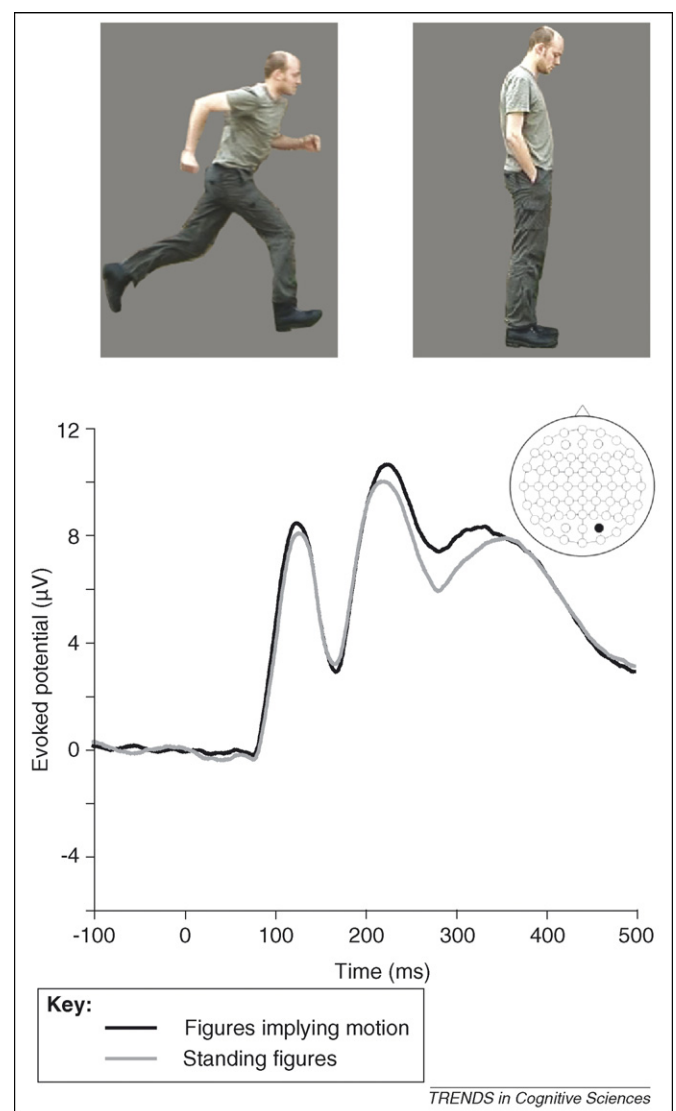

Figure 1. Animate motion from form. Human VEPs to images of human figures implying motion (black line) versus standing still (gray line) at one electrode position, resulting in the largest difference between 260 and 320 ms after stimulus onset, which is ~100 ms later than the response to real motion (data not shown). Modified, with permission, from [56].

Box 2. Functional relevance for form and motion interactions

Motion from form could well cause the sense of motion that we perceive while viewing static representations of motion, as present in photographs, sculptures and paintings. Furthermore, this process might help us to distinguish the movement of an animal, person or object against a moving background, and to track a moving person or object when the movement is intermittent due to occluding objects or eye blinks. The extra form information might increase motion sensitivity in low signal-to-noise situations. Furthermore, object motion is an important cue in the perception of actions by others. Human developmental studies have shown that even young children can already discriminate between pictures of objects implying motion and pictures of objects that do not imply motion [73], although this capability is still developing [74]. An interesting finding from these studies is that young children identify implied motion more accurately by postural cues than by conventional cartoon indicators of motion, such as speed lines behind a running person. Observation and even imagery of hands expressing implied motion induces an increase in corticospinal excitability for the muscles that would be involved in the observed action [75]. Thus, visual implied motion even affects motor and premotor areas, and therefore the neural network that processes motion from form might have an important role in shaping the activity of the mirror neuron system [63] that helps us to understand the intention of actions by others.

images with and without implied motion. Moreover, when processing in hMT+/V5 was disrupted by transcranial magnetic stimulation, the representational momentum effect was abolished [53]. Recent studies using magnetoencephalography (MEG) [54,55] and visual evoked potentials (VEPs) [56] in humans demonstrated a clear interaction between motion and form signals in the visual cortex (Figure 1). In particular, it was shown that the amplitude of an implied motion response was significantly reduced after adaptation to real motion in the same direction as the implied motion direction [57]. This adaptation indicates not only that form and motion are processed in the same cortical areas, but also that responses to implied motion arise from direction-selective neurons that are similarly tuned for real and animate implied motion directions.

Inanimate implied motion

The influence of low-level form cues on motion perception lends itself well to investigations in early motion-related areas. Krekelberg *et al.* [42] investigated the response of MT and MST neurons to Glass patterns (Figure 2a). These patterns are similar to motion streaks, in that they generate a percept of motion by the alignment of oriented elements along a common path. Single neurons in the prototypical macaque motion areas responded to these patterns as if they contain globally coherent motion
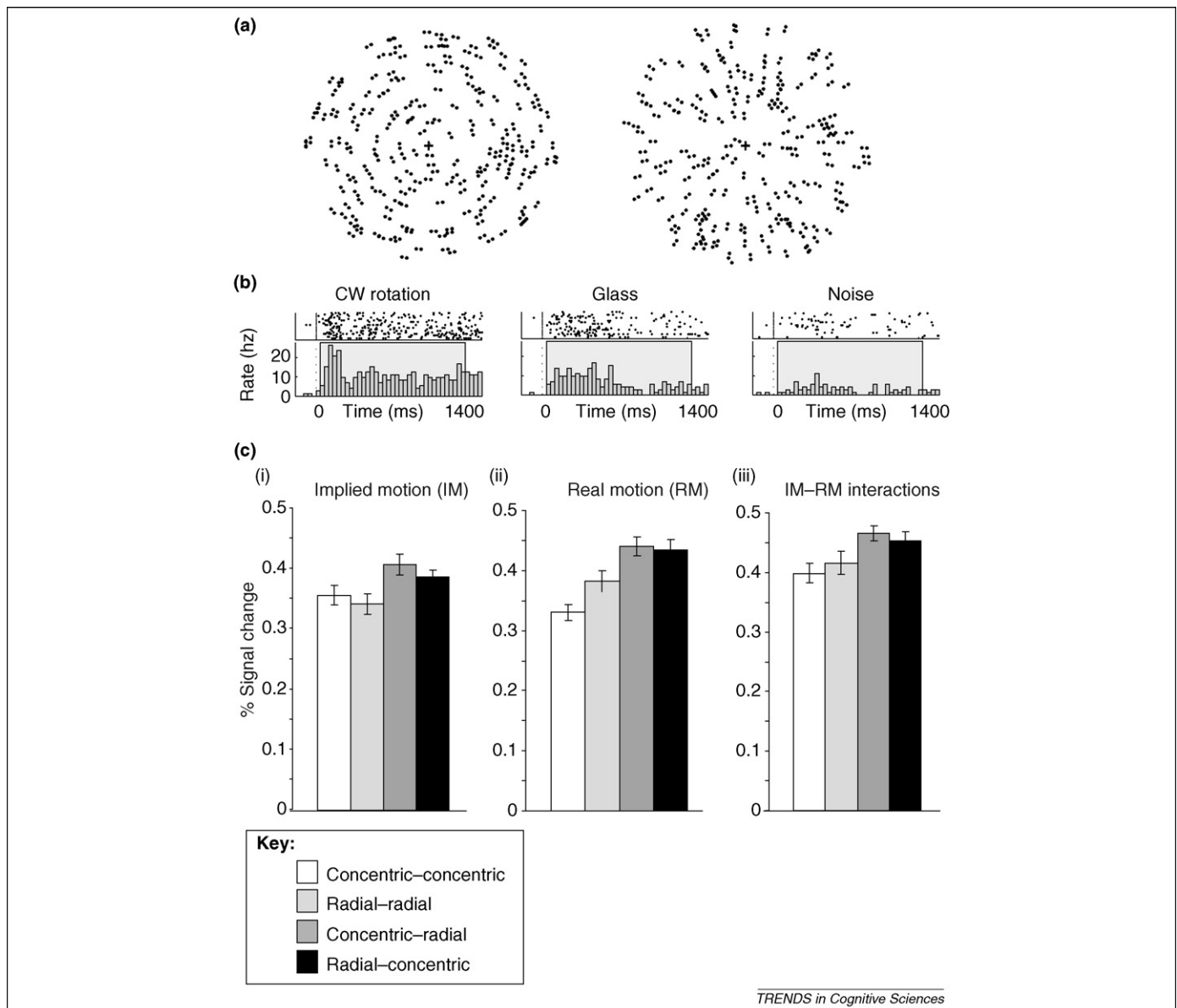

Figure 2. Inanimate motion from form. **(a)** Glass patterns are constructed by aligning static-oriented elements along a common path. A sequence of such patterns does not contain any net coherent motion energy but nevertheless evokes a motion percept consistent with the common path (e.g. rotation or expansion) [58]. Examples of rotation (left panel) and expansion (right panel) patterns are shown. **(b)** Implied motion responses in the macaque MT. Each dot in the raster plots represents a spike recorded from a single cell. The histograms represent the firing rate of the cell averaged over all trials. The gray shaded areas represent the time during which the stimulus was on the screen. (i) This shows the strong response to a clockwise (CW) rotating real motion pattern. (ii) This shows the weaker but significant response to a Glass pattern that implies a rotation. (iii) This shows the response to a pattern with randomly flickering dots. The cell responds to real motion and implied motion but not to random motion. Modified, with permission, from [42] **(c)** fMRI-selective adaptation for implied motion in hMT+/V5. fMRI responses for repeated presentation of the same stimulus pattern (concentric or radial) are lower than those for different global patterns presented in a sequence. This fMRI-selective adaptation in hMT+/V5 was observed for Glass patterns and real motion sequences. Interestingly, adapting to Glass patterns also induced adapted responses to real motion patterns of the same type (IM–RM Interactions), consistent with monkey physiology, showing MT cells that respond to real and implied motion. Modified, with permission, from [58].

(Figure 2b). Moreover, the cells had similar direction preferences for implied and real motion, and combining implied and real motion cues affected the response of the cells in a predictable manner that was consistent with the perceived motion direction. Imaging studies have confirmed these form and motion interactions in hMT+/V5 [58]. Using fMRI adaptation [59], these studies demonstrated that there is overlap between neural populations that respond differentially to the motion implied by different Glass pattern types (concentric versus radial) and populations responding to real concentric versus radial motion patterns (Figure 2c).

Neural mechanisms for form and motion interactions

Previous physiological studies have suggested that orientation-tuned V1 cells complete the first stage of the spatiotemporal integration of orientation signals (e.g. the oriented dot pairs in Glass patterns), which mediates the perception of the global structure [60]. It is possible that further analysis of these spatiotemporal correlations [61] in MT and MST mediates the perception of implied motion from low-level form cues (e.g. motion streaks, oriented dot pairs in Glass patterns). Thus, interactions between early visual analysis of spatiotemporal signals and neurons selective for coherent pattern motion in the MT and MST might mediate the perception of inanimate motion from form.

However, higher-level animate motion perception from static form cues entails interactions potentially between STS, motion-selective regions (MT and MST) and object-selective areas in the ventral cortex. Accumulating evidence from physiology and brain imaging suggests that the posterior STS might combine information about form and motion for the representation of biological percepts [62] and actions [63,64]. Further, whereas some models propose that biological motion perception need only make use of form information [65], others stress the integration of information from form-selective neurons in the ventral stream and optic flow detectors in the dorsal stream [66]. These findings suggest an important role for STS in the integration of form and motion information that might guide the perception of implied motion in static pictures and the understanding of actions.

Recent human electroencephalogram (EEG) and MEG studies shed light on the temporal characteristics of interactions between STS and hMT+/V5 [54–57], showing delayed responses (100 ms) to implied motion compared with real motion in hMT+/V5. These findings suggest that implied motion information arrives later than real motion in the dorsal motion-sensitive cortex, and that feedback projections from high-level form areas (e.g. STSa) might contribute to the processing of implied motion in low-level dorsal motion areas. Interestingly, anatomical connections between STS and parietal circuits suggest that information from STS might then be relayed to frontal motor and premotor regions that mediate action observation, imitation and execution [63,64]. Further, recent work provides evidence for functional interactions within this cortical circuit, showing distinct but interactive mechanisms for action understanding in the temporal, parietal and premotor cortex [67]. In particular, the ventral premotor cortex is shown to support the interpretation of actions and the acquisition of fine motor skills by encoding the physical differences between movement trajectories and their goals, whereas parietal and temporal areas are shown to encode the perceptually distinct features that enable us to discriminate between movements with different action goals and actors performing the same action in their personal style.

Conclusions

The integration of form and motion information is crucial for the unified perception of moving objects and for our successful interactions in complex and dynamic environments. In contrast to the proposed functional dissociation between shape- and motion-related areas in the ventral and dorsal neural pathways, the work reviewed here demonstrates extensive interactions between form and motion processing at multiple levels. In particular, both figural and low-level form cues affect motion perception, and motion cues can generate figural percepts. The integration of these cues is likely to take place at multiple levels in the cortex and involve recurrent connections between early visual areas engaged in the analysis of spatiotemporal statistics, higher ventral and dorsal regions that represent global form and motion, and frontoparietal circuits involved in the observation and execution of actions.

To delineate these interactions across cortical networks and unravel their functional roles, data acquired simultaneously from multiple areas, and with high temporal resolution, are needed. This is a difficult task for current methods when used in isolation, but combining multimodal imaging methods (fMRI, EEG and MEG) will enable further investigation of the global cortical networks involved in form and motion interactions and their dynamics. Further, combined fMRI studies on humans and monkeys will enable us to bridge the gap between imaging and neurophysiology findings across species and understand the neural mechanisms that mediate our perception of dynamic events at the scale both of large neural ensembles and the single neuron. In particular, identifying cortical regions involved in form and motion interactions in monkeys using fMRI and then investigating their processing with single cell recordings and microstimulation provides a unique approach for studying neural mechanisms across cortical areas. This combination of approaches has the power to reveal intriguing similarities and/or differences between cortical areas across species. For example, recent fMRI studies on the monkey showed that areas in the monkey STS (the lower superior temporal region, the FST region and the middle of the STP region) are involved in action-related movement [18]. Together with MT and MST, these cortical areas would be ideal candidates to target with physiological recordings for a mechanistic understanding of their functional role in form and motion perception.

Here, we have concentrated on evidence for cortical areas involved in the interaction between form and motion processing. This emphasis might suggest a static view of functionality associated with specific cortical centers, without considering how this functionality develops and

Box 3. The role of experience in shaping form and motion interactions

It is unclear how the visual system develops mechanisms that support form and motion interactions that are crucial for recognition and action in a dynamic environment. One possibility is that neural responses for motion from form result from associations in daily life because normally brief glimpses (snapshots) of moving objects are often accompanied by real motion. A recent study by Schlack and Albright [68] showed that some of these responses are learned. They trained macaques to associate an arbitrary static cue (e.g. a leftward pointing arrow) with real motion. Once the animal had learned the association, neurons in MT had acquired a direction-selective response to the static cues; they responded to leftward pointing arrows as if they contained leftward motion. A similar process could underlie other form-motion interactions. For instance, due to the retinal integration, a dot moving on the retina leaves behind it a trail of activation. This suggests that, over time, such comet tails could become associated with motion and might explain why motion streaks improve motion perception and why motion areas respond to the motion implied by Glass patterns. Thus, through evolution, development and life-long experience, the visual system becomes optimized in detecting statistical regularities in natural images [69,76] that mediate form and motion interactions and support our ability to interact fast and successfully in complex dynamic environments.

potentially changes flexibly with experience during the lifetime of a primate. Despite the importance of form and motion interactions for fast and successful recognition and action in a dynamic environment, little is known about the mechanisms that shape the anatomical and functional connectivity between form and motion processing. One possibility is that the visual system learns through experience to associate static object snapshots with motion because they frequently co-occur in natural images [68] (Box 3). Such statistical regularities reduce sensory redundancy and facilitate efficient decisions [69]. Further work (Box 4) is necessary to investigate the idea of an efficient adaptive code for spatiotemporal sequences in the primate brain and the role of experience-dependent plasticity in shaping this code [70,71]. A complete understanding of the interactions between form and motion processing will have to include not just where in the brain they take place, but why and how these interactions develop.

Box 4. Questions for future research

- What is the causal link between brain activity in motion- and form-related areas and the perception of animate or inanimate structure from motion and motion from form? Could stimulation of STS neurons cause the perception of motion in still images that do not imply motion?
- Does cortical damage or experimentally induced inactivation in circuits involved in action understanding result in deficits in motion and form integration?
- Do visuomotor experiences shape the functional interactions between cortical areas that mediate form and motion integration?
- How does the visual system combine low-level sensory input about form and motion with previous knowledge and expectations? Could prior knowledge influences on the interpretation of form and motion be implemented through feedback from higher areas to early stages of sensory processing?
- How does attention to higher-order information about actions affect processing in early motion-related areas?

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