



Recent advances in perception and action

1. Introduction

The relationship between perception and action is at the very focus of visual science. Since our sensory system provides the only way for us to guide our actions, it is necessary for sensory and motor systems to be closely coupled. Fortunately, during the past 20 years, the strict segregation between sensory science and motor science has been overcome. There were some important discoveries and theories that have stimulated the field tremendously. In this special issue of *Vision Research*, together with the accompanying first part (Gegenfurtner, Bremmer, Fiehler, Henriques, & Krauzlis, 2010), we present an overview of the field, 20 years after Mel Goodale and David Milner first proposed a functional dissociation between perception and action, based on evidence from neuropsychological patients (Goodale, Milner, Jakobson, & Carey, 1991) and psychophysics later (Aglioti, DeSouza, & Goodale, 1995).

The dual pathways theory of Goodale and Milner has been heavily debated in recent years (see Franz, 2001; Franz & Gegenfurtner, 2008; Goodale, *in press*; Goodale & Westwood, 2004; Milner & Goodale, 2008). In this issue, Westwood and Goodale (2011) review evidence from human neuropsychology and psychophysics about the relationship between action and perception. They arrive at the conclusion that the original claim of separate pathways for perception and action (Goodale & Milner, 1992) is still valid. They propose that many studies from human neuropsychology and psychophysics converge on the idea that action and perception are mediated by distinct but interacting visual systems. In contrast, Schenk, Franz, and Bruno (2011) argue that an integrative view of the visual cortex can explain both psychophysical and neuropsychological findings.

One of the reasons this debate has been going on for such a long time is that a large number of different studies have come up with diverging results. Therefore, Bruno, Knox, and de Grave (2010) used a meta-analysis on one particular visual illusion (Müller-Lyer) and one particular action (saccadic eye movements). They argue that many of the differences between studies can be ascribed to known factors modulating saccades and claim that their meta-analysis does not support a dissociation between conscious perception and oculomotor action. Similarly, Spering and Montagnini (2011) focus on one single aspect of perception and action, the relationship between motion perception and smooth pursuit eye movements. They argue that behavioral evidence points to similarities and differences between both responses, but that the dissociations might be due to differences in task requirements and temporal constraints.

Another interesting point is made by Schenk (2010). He argues that the motor system has access to a redundant set of visual information, and that this redundancy within the visuomotor system can explain visuomotor robustness after damage to the visual system. This redundancy basically means that spared capacity present after brain damage is hard to interpret. Beets *et al.* (2010) looked at online action-to-perception transfer in perceptual rivalry. They found that perception dependent actions are required for action-to-perception transfer. The interdependence they observed between action and perception supports common coding theory.

1. Grasping and reaching

The interaction between vision and action is particularly revealing in the arm motor system where the sensor and effector are separate. Scaling grip aperture while grasping objects appears to be highly influenced by changes and timing of the visual appearance of the object. Eloka and Franz (2011) found that when grasping an object, participants are able to adapt or incorporate perturbations in the shape of objects that occur both early and late in the movement. Yet, grasp accuracy and precision declines exponentially with increasing delays between viewing the object and grasping it (Hesse & Franz, 2010). Whitwell, Striemer, Nicolle, and Goodale (2011) show that a patient with blindsight following a unilateral V1 lesion can still correctly grasp objects that they cannot see nor even report the size using manual estimation, but only when grasping is immediate, but not following a delay. This suggests that vision may be processed differently depending on how and when this information is used. The results of Selen and Medendorp (2011) suggest that the location and orientation of objects for grasping are coded in a gaze-fixed reference frame. Several other studies in this issue provide support that spatial memory is coded and updated in gaze-fixed reference frame; when reaching to targets following various delays (Fiehler, Schütz, & Henriques, 2011), to sequential targets (Thompson & Henriques, 2010), when additional allocentric cues are available (Byrne, Cappadocia, & Crawford, 2010) and in other circumstances as reviewed by Thompson and Henriques (2011). Nonetheless when additional allocentric information is available, gaze-centered coding of reach targets is more likely to be combined with these gaze-independent representations. While previous studies have shown that the posterior parietal cortex is involved in remapping spatial memory as a function of gaze, Blangero *et al.* (2011) show the remapping that occurs when coding the goal of an anti-reach is processed differently as illustrated by the different pattern of errors produce by unilateral optical ataxic patients. The results of Klatzky, Wu, & Stet-

ten, 2010 also confirm that targets are localized better when the visual display is co-located in space with the action as compared to when the display is remote.

2. Eye movements

Vision is our dominant sense, and the relationship between vision and eye movements continues to provide a wealth of opportunities for probing the interplay between perception and action. Several studies in this special issue examine how smooth pursuit eye movements – the ability to track a moving object – interact with visual perception, and how internal ‘corollary discharge’ signals about smooth pursuit may contribute to visual perception. The review article by Bedell, Tong, and Aydin (2010) provides an authoritative overview of how the perceived smear of visual images is altered by eye and head movements, and also gives new evidence that perceived smear is not affected by visually induced self motion. Braun, Schütz, and Gegenfurtner (2010) show that subjects are better at detecting the change in speed of a moving target than in localizing where the change occurred, and that localization is strongly affected by the speed and direction of pursuit, implying that corollary discharge signals influence visual perception. Perceived locations are generally shifted in the direction of pursuit eye movements and Blanke, Harsch, Knöll, and Bremmer (2010) examined the time course of this mislocalization. They found that it starts before pursuit onset, again suggesting a role for corollary discharge in the perceptual effect. Schütz and Morrone (2010) found that perception of time is also affected by smooth pursuit, and is typically compressed compared to time perception during fixation. This holds for visual stimuli defined by luminance or color, but not for auditory stimuli. Together, these studies provide new insights into the possible functional roles of corollary discharge signals during the execution of smooth pursuit eye movements.

The issue of how visual inputs are processed for smooth pursuit, and how the system is able to track the correct visual object, remains an intriguing topic also addressed in this issue. By measuring receptive fields for pursuit, and also for motion perception, Debono, Schütz, Spering, and Gegenfurtner (2010) show that receptive fields for pursuit are centered on gaze position and that direction tuning during pursuit is narrow and aligned with the pursuit direction. Bogadhi et al. (2011) propose a model framework, based on Bayesian inference, for explaining how smooth pursuit initially follows the moving edges of a visual stimulus but over time is able to track the object’s global motion. Coppe, de Xivry, Missal, & Lefèvre, 2010 employ another modeling approach to test the contribution of biological motion inputs to smooth pursuit, and find evidence that biological motion contributes to the direct visual-motor pathways for pursuit. Mahaffy and Krauzlis (2011) conducted electrophysiological recordings from neurons in the frontal pursuit area, a brain region implicated in controlling the gain of smooth pursuit; they find that it is not involved in selecting the target object but is instead involved in forming the motor commands for pursuit.

The classic problem of how visual stability is maintained during saccades, despite abrupt retinal image shifts caused by saccades, is addressed by two papers in this issue. Klingenhoefer and Bremmer (2011) adopt a novel approach of studying how the stability of visual perception is affected during adaptation of saccade amplitude. They find that spatial perception changes in accord with the adaptive changes in saccades, but not with the variable changes in saccade amplitude that occur on a trial-by-trial basis. Cloherty, Mustari, Rosa, and Ibbotson (2010) investigate the neural basis of changes in visual perception during saccades, and report a surprising and striking effect in the activity of neurons in the dorsal medial superior temporal areas (MSTd):

visual responses are suppressed for stimuli around the time of saccades and enhanced for stimuli presented afterwards, but spontaneous activity tends to be enhanced during and immediately after saccades. This pattern of activity can contribute to perceptual stability despite the disruptions to the retinal image caused by each saccade.

This special issue also includes studies investigating how action and perception develops in young children. Libertus and Needham (2010) found that babies between the ages of 2 and 3 months showed greater progress in their reaching development when they practiced reaching (using Sticky mittens) compared to when they merely observed their parents’ actions. Paulus, Hunnius, and Bekkering (2011) showed that 20-month-old, but not 14-month-old, children are able to learn through observation that tools can have multiple purposes. The role of learning by observation helped 24 months old children (but not those 6 month younger) learn to grasp using comfortable posture with respect to the object heights and further helped 3-year olds with predicting the appropriate grip type (Jovanovic & Schwarzer, 2011). For navigating around obstacles during walking, Franchak and Adolph (2010) found that children between the ages of 4 and 8 fixated these obstacles more than adults who mainly relied on peripheral vision for navigating. The results of Franchak, van der Zalm, and Adolph (2010) showed that adult participants with prior experience (walking through doorways) made significantly more accurate decisions than those without, revealing a role of action feedback in facilitating judgments.

This issue also continues a fascinating discussion about the function and significance of “mirror neurons”, those neurons that tend to be equally responsive to the subject’s own actions as well as to the observation of similar actions of others. Zentgraf, Munzert, Bischoff, and Newman-Norlund (2011) expertly review a range of theoretical views on how these neurons may be involved in interpreting or understanding the actions of others, and also how these ideas can be applied in practical settings with athletes and patients. A study by Lindemann, Nuku, Rueschemeyer, and Bekkering (2011) shows how the sight of another person’s grasping movement can act as a powerful cue to shift attention, whereas an inanimate cue is not; this result suggests that spontaneous simulation of other’s actions may be an important control mechanism for visual attention.

Finally, the two last articles of this special issue are concerned with non-visual aspects of action and perception. Haptics has been at the forefront of research on perception and action, since our haptic system is essentially an active sensor (Klatzky & Lederman, 1999). Bergman Tiest (2010) reviews how we use our haptic senses to recognize material properties such as roughness, compliance, temperature and slipperiness. Di Luca and Mönter (2011) shows that compliance judgments depend on the relative amount of motion and force exerted—the finger that presses more contributes more to the final estimate.

Overall, we hope that the two parts of this special issue can give an indication of this exciting, stimulating and heavily debated field of research!

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