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Grasping for parsimony: Do some motor actions escape dorsal processing?

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ABSTRACT

It is an open question whether the visual transformations guiding human actions are similar to those generating visual perception. The Action–Perception model assumes a strict division of labor: the ventral cortical stream generates perception while the dorsal stream guides actions. However, only skilled and natural actions are assumed to be under dorsal control, while awkward and left-handed actions should be under ventral control in the same way as perception. Here, we used a combination of Garner-Interference and the psychological refractory period (PRP) paradigm to test this notion. We found that all types of grasping (left-handed, awkward, using a tool) behave in a way similar to skilled right-handed grasping: other than perception they show no Garner-Interference, but similar to perception they show a limitation of processing capacities as indicated by the PRP paradigm. This behavior suggests that similar processes guide all these actions.

In every second the human brain processes a huge amount of visual information. On the one hand we regularly need to identify objects in our surroundings, and on the other hand we also need to visually guide ourselves through space. The Action–Perception model attributes these two purposes to two different anatomical pathways (Goodale & Milner, 1992; Milner & Goodale, 2006): the ventral 'vision for perception' system is assumed to generate the visual percept, while the dorsal 'vision for action' system is assumed to guide motor actions. However, not all actions are assumed to be under dorsal control. Only if an action is highly skilled and "natural", the dorsal stream can be exploited. If an action is unskilled or performed in an awkward and unskilled way, it is assumed that the more flexible processing of the ventral stream will guide this action. The aim of our study was to shed some light on this notion and our results question that such a switch from dorsal to ventral control takes place.

In the next sections, we will first sketch the Action–Perception model, then we will discuss behavioral markers for dorsal versus ventral processing, and finally we show how we applied these markers to left-handed, unskilled, and awkward actions that are in the traditional view of the Action–Perception model exceptions from dorsal processing. Surprisingly, we found for all these actions a similar pattern of results as for highly skilled, right-handed actions. These results are inconsistent with the notion that different processing streams control certain classes of actions.

1. The Action–Perception model

Among the most prominent and extensively investigated topics in visual sciences and cognitive psychology is the distinction into a 'ventral' and a 'dorsal' pathway of visual processing: both pathways process roughly the same visual input and start their projections from the primary visual cortex (V1). Then the dorsal pathway terminates in posterior parietal areas, while the ventral pathway terminates in inferior temporal areas. Following earlier models that ascribed to these pathways different functions in processing spatial *vs.* identity information (Ungerleider & Mishkin, 1982), the currently most influential model is the Action–Perception model by Goodale and Milner (1992) and Milner and Goodale (2006). According to this model the purpose of the ventral pathway is the perceptual identification of stimuli ('vision for perception'), while the dorsal pathway serves to program and control visually guided motor actions ('vision for action'). In other words: both pathways analyze the same visual input but for different purposes. The initial evidence for this model came from the neuropsychological double dissociation of (visual (form) agnosia) and optic ataxia. Visual agnostic patients, suffering from lesions to ventral occipito-temporal areas, are typically not able to recognize or discriminate between objects, but at the same time have no (or only few) problems acting on them. The opposite pattern is found in optic ataxic patients, suffering from lesions in dorsal stream areas of the posterior parietal cortex. These patients have no problems discriminating

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or recognizing objects, but exhibit marked problems when, e.g., grasping them. Other lines of evidence have been proposed subsequent to the initial formulation of the Action–Perception model, among them are results from imaging studies and the different effect of visual illusions on perception and action—which will be discussed in greater detail below (see Milner & Goodale, 2006, for an exhaustive review of evidence). The Action–Perception model soon became influential and extremely fruitful in producing testable hypotheses.

How can we decide whether a given task was carried out with the help of the dorsal or the ventral pathway in a behavioral experiment? At present two suggestions exist in the literature: the dissociable effects of visual illusions on dorsal and ventral tasks (e.g., Aglioti, DeSouza, & Goodale, 1995), and the use of Garner-Interference which indicates ventral processing (Ganel & Goodale, 2003). We will discuss these two methods successively.

2. Visual illusions as behavioral markers of ventral *vs.* dorsal processing

The Action–Perception model ascribes to the ventral pathway an allocentric and to the dorsal pathway an egocentric coding of spatial coordinates. This allows for an interesting prediction concerning the influence of visual illusions in non-clinical populations and thus to gather support for the Action–Perception model from experiments with healthy participants: certain visual (size) illusions should only have an effect on the performance in tasks guided by ventral mechanisms (e.g., judging the size of the inner circle in the Ebbinghaus illusion); while the same illusions should have no effect on tasks where the dorsal pathway carries out the bulk of work (e.g., grasping the inner circle of the Ebbinghaus illusion with a precision grip, i.e., between the thumb and the index finger). A suitable dependent measure in latter tasks is the maximum grip aperture (MGA; i.e., the maximal distance between thumb and index-finger in-flight) which is achieved after about two thirds of a grasping movement, and is linearly related to the size of the target object. Aglioti et al. (1995) were the first to test this prediction and they interpreted their results as supporting the Action–Perception model. Subsequently, this line of research attracted many studies and the basic pattern was replicated several times (e.g., Haffenden & Goodale, 1998; Haffenden, Schiff, & Goodale, 2001). However, other researchers came to opposite conclusions. Indeed, in many studies there is a positive effect of visual illusions on grasping (Franz, 2001; Franz & Gegenfurtner, 2008) which is not predicted by the Action–Perception model. Importantly, this effect seems not being due to other mechanisms like obstacle-avoidance during the grasp (Franz, Bülthoff, & Fahle, 2003). Moreover, whether or not grasping and perceptual measures are differently affected by illusions seems to depend on two conditions. First, the perceptual measure needs to be calibrated adequately. For example, the perceptual measure "manual size estimation" responds to any variation of object size – be it illusionary or non-illusionary – much stronger than grasping does. To take this adequately into account, certain corrections are necessary, and if these corrections are performed, there doesn't seem to be a difference between illusion effects in perception and action (Franz, 2003; Franz & Gegenfurtner, 2008). Secondly, the grasping and perception tasks need to be equal in terms of task demands (e.g., attentional demands). Studies with a good match across both tasks repeatedly found no difference between the illusion effects on grasping and perception (e.g., Franz et al., 2003; Franz, Gegenfurtner, Bülthoff, & Fahle, 2000; Pavani, Boscagli, Benvenuti, Rabuffetti, & Farnè, 1999). But this debate is far from resolved (for recent summaries see Franz & Gegenfurtner, 2008 and Goodale, 2008) such that it seems beneficial to search for other behavioral markers for dorsal and ventral processing.

3. Garner-Interference as a behavioral marker of ventral *vs.* dorsal processing

An alternative behavioral indicator for the dichotomy of dorsal versus ventral processing can be derived from the study by Ganel and Goodale (2003). According to these authors the dorsal pathway is able to process its input in an analytical fashion, while the ventral pathway processes the input holistically. In other words: the dorsal pathway should be able to ignore variations of task-irrelevant stimulus dimensions, while this should not be true for the ventral pathway. As a consequence, this should give rise to interference phenomena when task-irrelevant stimulus dimensions are varied in addition to the task-relevant characteristics. This has been demonstrated by Ganel and Goodale (2003) in an elegant way using a variant of Garner's speeded classification task (Garner, 1978; Garner & Felfoldy, 1970). In their experiments four small wooden blocks resulting from a factorial combination of two widths (30 mm *vs.* 35.7 mm) and lengths (63 mm *vs.* 75 mm) were used as stimuli. In the grasping task (presumably a typical dorsal task), participants were to grasp the stimulus blocks across their width with a precision grip, in the perceptual judgment task (presumably a typical ventral task) the participants were to judge the blocks' width. Thus, the width was the relevant stimulus dimension for both tasks. Importantly, both tasks were performed under two experimental conditions. (1) In the 'baseline' condition only the two stimulus blocks of the same length were used, i.e., the irrelevant length dimension was constant. (2) In contrast, in the 'filtering' condition all four stimulus blocks were used, and thus the irrelevant dimension also varied. As predicted, this task-irrelevant variation produced interference only in the perceptual judgment task, where response times were higher in the filtering condition than in the baseline condition (i.e., 'Garner-Interference'). In the grasping task, however, no differences in response times (and in movement trajectories) were found. To the extent that the underlying logic is correct Garner-Interference can serve as an alternative behavioral indicator: if a task relies on ventral processing, Garner-Interference should emerge.

4. The psychological refractory period (PRP) paradigm as a marker of resource-limited processing

According to the Action–Perception model, dorsal processing should be automatic and independent of ventral processing. Therefore, performance in a typical dorsal task (like grasping) should not suffer if performed in parallel to a typical ventral task (like pitch discrimination). This notion was the main focus of two recent studies by Kunde, Landgraf, Paelecke, and Kiesel (2007) and Janczyk and Kunde (2010) who used a classical dual-task situation, the PRP paradigm.[1] The results of these studies show that both grasping and the perceptual judgment task of Ganel and Goodale (2003) operate in a capacity-limited, non-automatic way. Interestingly, Kunde, Landgraf, et al. (2007) and Janczyk and Kunde (2010) combined their PRP paradigm with the Garner-Interference paradigm of Ganel and Goodale (2003). Replicating Ganel and Goodale (2003), they found Garner-Interference only in the perceptual judgment of the stimulus blocks width, but not when grasping these same blocks. Thus, Garner-Interference appears suitable as

[1] The present Experiments 1, 2 and 4 were – for reasons laid out in the introduction to Experiment 1 – settled within the PRP paradigm, too, and assume the existence of a central response selection bottleneck (Pashler, 1994; Pashler & Johnston, 1998; Welford, 1952). However, the focus of this study is not the dual-task behavior of motor actions and we thus omitted a detailed theoretical account and description in the main part of the text. See also Appendix A and further in-depth treatments of these topics (e.g., Pashler, 1994; Pashler & Johnston, 1998).