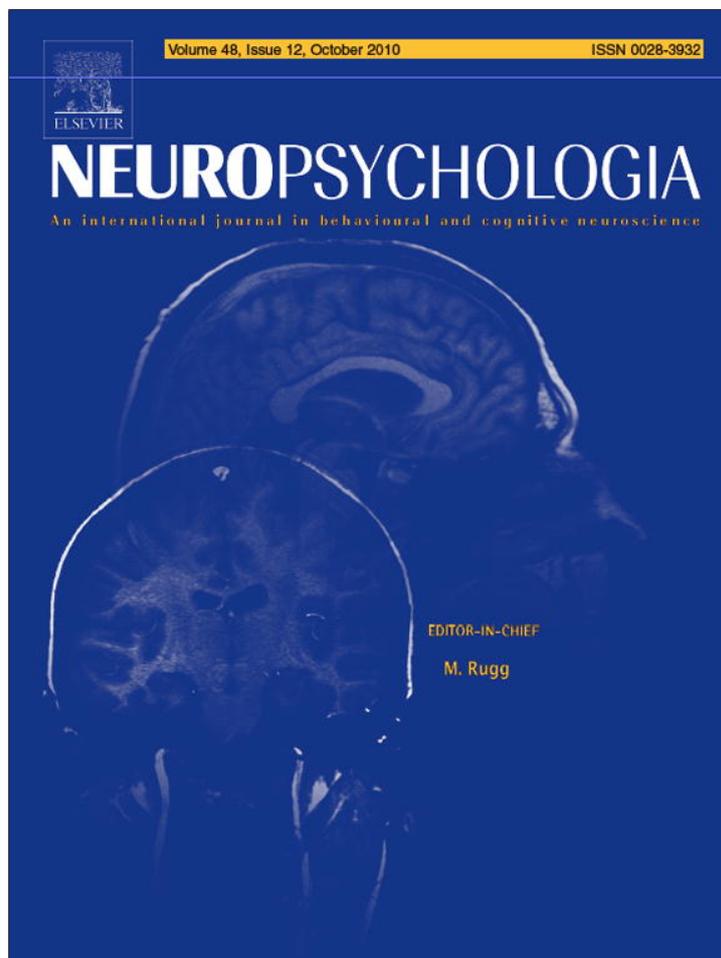


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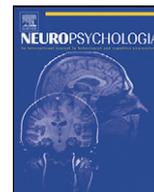
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## Grasping for parsimony: Do some motor actions escape dorsal processing?

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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.

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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, Bühlhoff, & 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 illusory or non-illusory – 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, Bühlhoff, & 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.<sup>1</sup> 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

<sup>1</sup> 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).

a behavioral indicator for ventral processing—even under dual-task situations.

### 5. Are some actions under ventral control?

From its very outset, the Action–Perception model assumed that certain actions are under ventral control. This idea bears on the fact that, for example, the famous patient D.F. performs normal grasping along the width of an object (interpreted as intact visual input to the dorsal stream), but is not able to indicate the width with her fingers (Goodale & Milner, 1992). Indicating the width with the fingers is therefore interpreted as being ventrally controlled. Because the visual input to the ventral stream is assumed to be damaged, the Action–Perception model therefore can explain D.F.'s deficit. In general, all actions that are not highly skilled and are not performed on easily available visual input are assumed to be controlled by the ventral stream. This includes mimicked actions (Goodale, Jakobson, & Keillor, 1994), actions that are performed after the visual input has been removed from sight (Goodale, Westwood, & Milner, 2004), awkward and unskilled actions (Gonzalez, Ganel, Whitwell, Morrissey, & Goodale, 2008), and left-handed<sup>2</sup> actions (Gonzalez, Ganel, & Goodale, 2006).

If this is true, then it is an important question to determine exactly which visually guided actions are under dorsal control, and which are not—not only for psychological theorizing, but for applied purposes as well. Consider, for example, that in modern working environments many motor tasks produce effects in the environment that are transformations of the natural movements of the hand or the fingers. This is the case with physical tools, such as levers or grippers, as well as with “virtual” tools such as a computer-mouse or other pointing devices (e.g., Kunde, Müsseler, & Heuer, 2007). Without knowing whether such artificial actions are constrained by the same factors as natural actions, it is impossible to evaluate their ergonomic value or to identify conditions that render them error-prone.

Therefore, we used a sample of relevant actions that might be under ventral control and tested them using the combined PRP and Garner-Interference design as developed by Kunde, Landgraf, et al. (2007). In Experiment 1 we tested left-handed grasping in right-handers, in Experiments 2 and 3 we tested awkward grasping, and in Experiment 4 unskilled grasping using a tool. This subset of actions is of particular interest since they all aim at directly interacting with a target stimulus and can be visually guided with available input. As such they are good candidates for dorsal processing, but still have been suggested to be guided by the ventral stream (Gonzalez, Ganel, et al., 2006; Gonzalez et al., 2008). If any of these actions is indeed under ventral control, we would expect Garner-Interference.

## 6. Experiment 1

In this experiment, we tested whether left-handed (precision) grasping is under ventral control, as suggested by Gonzalez, Ganel, et al. (2006). Evidence for this proposal came from an effect of visual illusions on grasping with the left but not with the right

hand. We have argued that the (non-) existence of effects of visual illusions on grasping is still quite controversial (Franz & Gegenfurtner, 2008; Goodale, 2008). This in turn prompts the search for converging evidence using a different indicator, such as Garner-Interference introduced above. If left-handed grasping indeed relies more on perceptual information provided by the ventral pathway (as opposed to the dorsal system, which applies for right-handed precision grasping) this should result in Garner-Interference.

Experiment 1 (and also the following Experiments 2 and 4) is settled within the PRP paradigm for mainly two reasons. First, we have shown elsewhere that a (dorsal) right-handed precision grasp is subject to the PRP effect, i.e., relies on central resources (Janczyk & Kunde, 2010; Kunde, Landgraf, et al., 2007). For better comparability with these studies and to generalize this finding to other classes of grasping movements, we applied the PRP paradigm here, too. Second, in previous work the Garner-Interference observed in the perceptual judgment tasks combined additively with the dual-task factor stimulus onset asynchrony (SOA; Janczyk & Kunde, 2010, Experiment 1; Kunde, Landgraf, et al., 2007). According to the PRP logic and the central bottleneck model (see Appendix A; Pashler, 1994; Pashler & Johnston, 1998) this suggests an implication of central attention to resolve Garner-Interference. At first glance, this appears somewhat counterintuitive since Garner-Interference can be seen as a perceptual effect (which should result in an underadditive combination with SOA; see Pashler, 1994, or Pashler & Johnston, 1998). The use of the PRP paradigm thus enables us to assess whether this finding also applies to the classes of movements under investigation here, insofar as they produce Garner-Interference.

### 6.1. Method

#### 6.1.1. Participants

Sixteen undergraduates from Dortmund University of Technology (2 male, mean age = 24;0 years) participated in return of course credit. All participants were right-handed (by self-report) and had normal or corrected-to-normal vision.

#### 6.1.2. Design, apparatus, and stimuli

Each participant was tested in a single-session PRP experiment of about 60–75 min. Task 1 was a binary tone classification task and was responded to with a right hand key press. Stimuli (S1) were two 50 ms tones presented via headphones (low tone: 300 Hz; high tone: 900 Hz). Task 2 was a grasping task, where participants grasped a stimulus across its width using a left-handed precision grip (i.e., between thumb and index-finger of the left hand). Stimuli in this task (S2) were four small wooden blocks constructed according to a factorial combination of two widths (30 mm and 35.7 mm) and two lengths (63 mm and 75 mm). S2 visibility was controlled by using computer controlled PLATO shutter glasses (Translucent Technologies) and the stimuli were presented on a small custom-made table where they depressed a hidden micro switch. To avoid misunderstandings here: participants did not preview the to-be-grasped stimuli and started the grasping movement upon a go-signal. Rather, the shutter glasses opened and provided view of the stimuli after the SOA, and participants were then to start their grasping movement. As such, the grasping movement was not an instance of delayed movements, which have been described to rely on perceptual information provided by the ventral stream (e.g., Hu & Goodale, 2000). The grasping movements were performed closed-loop. This was done to make the experiments comparable to the studies by Ganel and Goodale (2003), Gonzalez, Ganel, et al. (2006) and Gonzalez et al. (2008). Note that in supplementary material, Ganel and Goodale (2003) reported a control experiment where grasping was performed open-loop, with similar results as

<sup>2</sup> The reader might be tempted to add: “in right-handers”, but this would not correctly reflect the theory. Gonzalez, Ganel, et al. (2006) and Gonzalez, Goodale, et al. (2006) did indeed claim that even in left-handers only right handed actions are controlled by the dorsal stream, thereby implying that left handers cannot exploit the evolutionary advantages of the dorsal stream as long as they are using their dominant, left hand. Of course, this is a very strong claim that has been criticized heavily (Derakhshan, 2006) and Gonzalez, Goodale, et al. (2006) admitted in a reply that this was only a “tentative idea”. Because we don't want to build up a straw-man, we will, for the purposes of this paper, only consider the more cautious assumption that left-handed actions in right-handers are controlled by the ventral stream.

those from the closed-loop condition. The response time in Task 1 (RT1) was measured from tone presentation until the right hand key press. Response time in Task 2 (RT2) was measured from the shutter glasses opening until the left index-finger left a home button. The time from this event until when the target S2 was lifted was measured as the movement time (MT).

6.1.3. Procedure

The whole experiment comprised one short practice block (24 trials) followed by four experimental blocks of 72 trials each. Of the experimental blocks, two were 'baseline' conditions in which only the two S2 stimulus blocks of the same length were used, the remaining blocks were 'filtering' conditions in which all four possible S2 stimulus blocks were used. Prior to every block, participants were shown those S2 stimuli used in the upcoming block, and were asked to thoroughly inspect them. Four orders of experimental blocks were applied, resulting from counterbalancing the two baseline and the two filtering conditions with the order of the two possible baseline conditions also counterbalanced. Each trial began with a short warning click, and 1000ms later S1 was played. Following a varying SOA of 50, 500, or 1000ms the shutter glasses opened and provided view of S2. Task 1 errors were detected automatically, Task 2 grasping accuracy was judged by the experimenter (only a precision-grip was judged correct). The experimenter gave feedback after each trial. After the participant placed the left index-finger back on the home-button, the shutter glasses became opaque, and the experimenter prepared the next trial. Participants received written instructions prior to the experiments proper which emphasized speed and accuracy. Task 1 performance was given priority over Task 2.

The order of experimental blocks (4) and the stimulus-response-mapping of Task 1 (2) were counterbalanced across participants. Each baseline condition block comprised 2 (Task 1 stimuli) × 2 (Task 2 stimuli) × 3 (SOA) × 6 (repetitions) trials presented in a random order; filtering condition blocks comprised 2 (Task 1 stimuli) × 4 (Task 2 stimuli) × 3 (SOA) × 3 (repetitions) trials presented in a random order.

6.1.4. Data treatment and analyses

Analyses were mainly done by means of analysis of variance (ANOVA) with the factors condition (baseline vs. filtering) and SOA (50 ms vs. 500 ms vs. 1000 ms) as repeated measures (if necessary, Greenhouse-Geisser corrections were applied and the corresponding  $\epsilon$  is reported). It is a significant effect of condition that would signal the presence of Garner-Interference in all here reported experiments. For all statistical analyses a significance level of  $\alpha = .05$  was used throughout this paper and sample effect sizes are reported as partial  $\eta^2$ . (We ran all analyses again after applying the log-transformation to RT/MT data. Overall, this gave the same results as the analyses using raw RT/MT data—for the only exception see the Results section of Experiment 4.)

Trials with general errors (e.g., too slow responses, leaving the home button prior to the glasses' opening, etc.) were excluded from all analyses. The reported error analyses are based on Task 1 and Task 2 accuracy of the remaining trials. For RT analyses only those trials were included where both tasks were responded to correct. Furthermore, RTs less than 150 ms (anticipations) or exceeding the individual's mean by more than 2.5 individual standard deviations (calculated separately for each participant and analyzed condition; outliers) were excluded (Task 1: 2.9%; Task 2: 4.2%).

6.2. Results

Of primary importance for the present research are the results from the grasping task (Task 2). We thus present

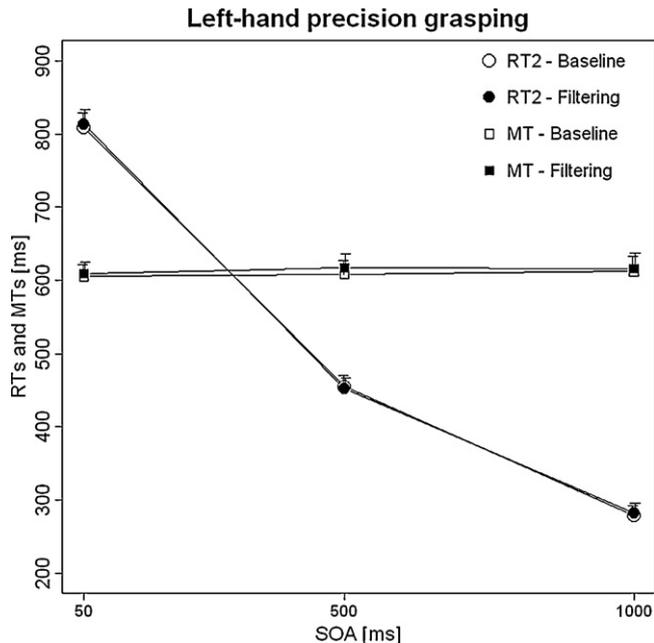


Fig. 1. Mean response times (RTs) and movement times (MTs) in milliseconds for the left-handed grasping task (Experiment 1) as a function of SOA (stimulus onset asynchrony) and condition.

these first, followed by a brief presentation of the Task 1 results.

6.2.1. RT and MT analyses

Mean RTs and MTs in Task 2 are visualized in Fig. 1. As can be seen, RT2 showed a large increase with a decreasing SOA—from about 250 ms at the longest SOA to 800 ms at the shortest SOA (the PRP effect). However, there is not much of an RT difference between baseline and filtering conditions. The corresponding ANOVA confirmed only the effect of SOA as significant;  $F(2,30) = 756.76, p < .01$ , partial  $\eta^2 = .98, \epsilon = .71$ . Neither the effect of condition;  $F(1,15) = 0.02, p = .89$ , partial  $\eta^2 < .01$ ; nor the interaction SOA × condition;  $F(2,30) = 0.28, p = .69$ , partial  $\eta^2 = .02, \epsilon = .71$ ; were significant. MTs showed only a small variation between 642 and 666 ms, thus they were roughly at one level independent of SOA and condition. The ANOVA on MTs revealed no effect as significant; SOA:  $F(2,30) = 3.16, p = .08$ , partial  $\eta^2 = .17, \epsilon = .64$ ; condition:  $F(1,15) = 1.03, p = .33$ , partial  $\eta^2 = .06$ ; interaction SOA × condition:  $F(2,30) = 0.05, p = .95$ , partial  $\eta^2 < .01$ .

Mean RTs in Task 1 (see Table 1) showed a slight and significant increase with an increasing SOA;  $F(2,30) = 9.28, p < .01$ ,

Table 1 Response times to Task 1 in milliseconds from Experiments 1, 2 and 4 as a function of SOA (stimulus onset asynchrony) and condition.

	Condition	SOA		
		50	500	1000
Experiment 1 (left-handed grasping)	Baseline	593	644	691
	Filtering	597	636	675
Experiment 2 (awkward grasping)	Baseline	369	389	397
	Filtering	375	406	440
Experiment 4 (perceptual judgment)	Baseline	636	608	644
	Filtering	667	633	672
Experiment 4 (tool grasping)	Baseline	454	504	539
	Filtering	475	525	572

partial  $\eta^2 = .38$ ,  $\varepsilon = .55$ . No other effect was significant; condition:  $F(1,15) = 0.22$ ,  $p = .64$ , partial  $\eta^2 = .02$ ; interaction SOA  $\times$  condition:  $F(2,30) = 1.39$ ,  $p = .26$ , partial  $\eta^2 = .09$ ,  $\varepsilon = .64$ .

### 6.2.2. Error analyses

Mean error percentages in both tasks are presented in Table 2, and detailed statistics are summarized in Table 3. In general, Task 2 errors were rare and showed no systematic variation with either factor or the respective interaction. In contrast, Task 1 errors were overall higher and showed a significant decrease with an increasing SOA.

### 6.3. Discussion

Experiment 1 was run to assess whether left-handed grasping (in right-handers) relies on ventral instead of on dorsal processing, as suggested by Gonzalez, Ganel, et al. (2006). If left-handed grasping is indeed under ventral control, Garner-Interference (i.e., an RT difference between baseline and filtering conditions) should emerge. In addition to Garner-Interference, we tested for a PRP effect with a binary tone classification as Task 1. As Task 2 participants used a left-handed precision grip to grasp a stimulus block across its width.

First, the data show the typical pattern observed in PRP experiments. Whereas RT1 was largely unaffected by any manipulation (the small increase with an increasing SOA may even be due to a speed-accuracy trade-off), RT2 decreased about 500 ms with an increasing SOA—a finding well known as the PRP effect. Previous reports of non-automatic dorsal processing of grasping (Janczyk & Kunde, 2010; Kunde, Landgraf, et al., 2007) thus generalize to left-handed grasping.

Second, and of more importance, RTs did not differ between baseline and filtering conditions. In other words: we found no Garner-Interference for left-handed grasping, indicating that the involved planning mechanisms were able to efficiently ignore the task-irrelevant variation of the stimuli' length. Crucially, this ability has been ascribed to the dorsal pathway (Ganel & Goodale, 2003), and thus using Garner-Interference as the indicator leads to a conclusion contrasting the one by Gonzalez, Ganel, et al. (2006): we need to conclude that there is no difference between left- and right-handed precision grasping in right-handers.

## 7. Experiment 2

In Experiment 1 we used Garner-Interference instead of the absence or presence of visual illusory effects to assess whether left-handed grasping is indeed under ventral instead of dorsal control (Gonzalez, Ganel, et al., 2006; Gonzalez, Goodale, et al., 2006). The results were not supportive; rather they point to a recruitment of processes similar to those that have been observed for right-handed grasping (Ganel & Goodale, 2003; Janczyk & Kunde, 2010; Kunde, Landgraf, et al., 2007).

Recently, a second candidate action relying on ventral instead of dorsal processing has been identified, namely unskilled actions (Gonzalez et al., 2008). Experiment 2 resembles Experiment 1, but the participants used an 'awkward grip' (they grasped the target stimulus using their thumb and ring-finger) with their right hand. Again, we tested whether Garner-Interference might indicate a ventral mode of processing for this kind of action.

### 7.1. Method

#### 7.1.1. Participants

Sixteen new undergraduates from Dortmund University of Technology (3 male, mean age = 22;4 years) participated in return

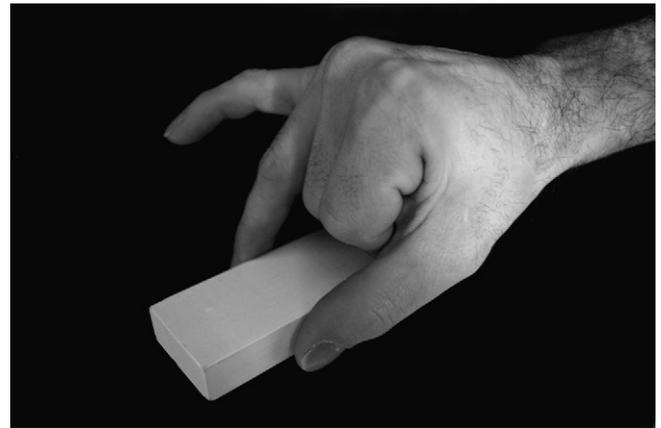


Fig. 2. Illustration of the awkward grasping task used in Experiments 2 and 3.

of course credit. All participants were right-handed (by self-report) and had normal or corrected-to-normal vision.

#### 7.1.2. Design, apparatus, stimuli, procedure, data treatment, and analyses

This experiment was very similar to Experiment 1, and we therefore only introduce the major changes. In this experiment participants were asked to grasp the stimulus blocks across their width using an 'awkward grip' of the right-hand (i.e., between their thumbs and ring-finger; Gonzalez et al., 2008; see Fig. 2). As a consequence, the home button was now depressed with the index-finger of the right hand, and the responses to Task 1 were given with the left hand. 3.3% and 3.3% of the trials were excluded as outliers in Tasks 1 and 2, respectively.

### 7.2. Results

#### 7.2.1. RT and MT analyses

Mean RTs and MTs in Task 2 are visualized in Fig. 3. Compared with the results of Experiment 1 (see Fig. 1), there are striking sim-

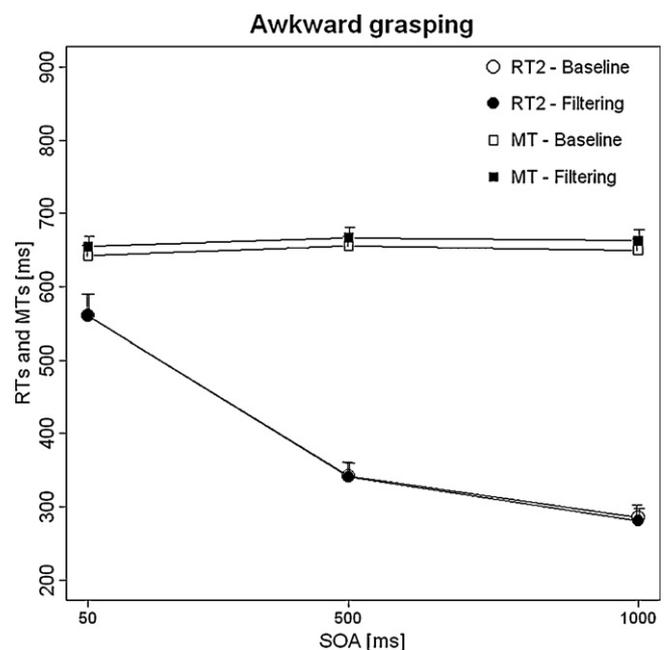


Fig. 3. Mean response times (RTs) and movement times (MTs) in milliseconds for the awkward grasping task (Experiment 2) as a function of SOA (stimulus onset asynchrony) and condition.

**Table 2**  
Mean error percentages in Tasks 1 and 2 from Experiments 1, 2 and 4 as a function of SOA (stimulus onset asynchrony) and condition.

	Condition	Task 1			Task 2		
		SOA			SOA		
		50	500	1000	50	500	1000
Experiment 1 (left-handed grasping)	Baseline	4.2	1.8	2.2	1.2	1.0	0.8
	Filtering	3.7	2.0	1.4	0.7	0.5	0.6
Experiment 2 (awkward grasping)	Baseline	2.6	2.2	1.8	0.3	0.3	0.7
	Filtering	3.2	3.0	2.7	0.3	0.3	0.5
Experiment 4 (perceptual judgment)	Baseline	3.1	2.0	2.4	6.4	4.5	5.8
	Filtering	2.5	1.7	2.2	9.1	9.1	8.1
Experiment 4 (tool grasping)	Baseline	3.5	2.4	2.3	3.4	4.1	4.2
	Filtering	3.8	2.8	2.0	4.0	4.3	4.1

**Table 3**  
Detailed statistics on mean error percentages in Tasks 1 and 2 for Experiments 1, 2 and 4. Degrees of freedom (*dfs*) are given as “numerator's, denominator's *dfs*”, sample effect sizes are given as partial  $\eta^2$ , and significant *F*-ratios are marked with an asterisk (\*).

	Task 1			Task 2		
	<i>F</i>	<i>dfs</i>	part. $\eta^2$	<i>F</i>	<i>dfs</i>	part. $\eta^2$
Experiment 1						
SOA	5.66*	2.30	.27	0.37	2.30	.02
Condition	0.75	1.15	.05	3.29	1.15	.18
SOA × Condition	0.27	2.30	.02	0.34	2.30	.02
Experiment 2						
SOA	0.61	2.30	.04	3.43*	2.30	.19
Condition	2.48	1.15	.14	0.14	1.15	.01
SOA × Condition	0.07	2.30	<.01	0.07	2.30	.01
Experiment 4						
SOA	5.82*	2.62	.16	0.23	2.62	.01
Condition	0.21	1.31	.01	12.28*	1.31	.28
Task	2.03	1.31	.06	12.19*	1.31	.28
SOA × Condition	0.16	2.62	.01	1.99	2.62	.06
SOA × Task	1.92	2.62	.06	2.02	2.62	.06
Condition × Task	1.43	1.31	.04	5.66*	1.31	.15
SOA × Condition × Task	0.47	2.62	.02	1.66	2.62	.05

# *p* = .07.

ilarities. Again, RT2 dropped several hundred milliseconds when the SOA increased, thus showing the typical PRP effect. Moreover, there was again no difference between baseline and filtering conditions, i.e., no Garner-Interference. The ANOVA confirmed the effect of SOA as significant;  $F(2,30) = 157.29, p < .01$ , partial  $\eta^2 = .91, \epsilon = .61$ ; but neither was the effect of condition significant;  $F(1,15) = 0.02, p = .89$ , partial  $\eta^2 < .01$ ; nor was the interaction SOA × condition;  $F(2,30) = 0.06, p = .94$ , partial  $\eta^2 < .01$ . MTs showed only little variation between 605 ms and 617 ms, and no effect reached significance in the respective ANOVA; SOA:  $F(2,30) = 1.31, p = .27$ , partial  $\eta^2 = .08, \epsilon = .57$ ; condition:  $F(1,15) = 0.36, p = .56$ , partial  $\eta^2 = .02$ ; interaction SOA × condition:  $F(2,30) = 0.84, p = .41$ , partial  $\eta^2 = .05, \epsilon = .69$ .

Mean RTs in Task 1 (see Table 1) significantly increased with an increasing SOA;  $F(2,30) = 10.11, p < .01$ , partial  $\eta^2 = .40, \epsilon = .70$ . No other effect was significant; condition:  $F(1,15) = 3.65, p = .08$ , partial  $\eta^2 = .20$ ; interaction SOA × condition:  $F(2,30) = 2.28, p = .12$ , partial  $\eta^2 = .13$ .

### 7.3. Error analyses

Mean error percentages are presented in Table 2 and detailed statistics are summarized in Table 3. In general, error rates were low in both tasks, but extremely low in Task 2. Mean error percentages in Task 1 showed no reliable variation with either factor. For Task 2, however, there was a small, but nonethe-

less, significant increase in error rates at the highest SOA of 1000 ms.

### 7.4. Discussion

In Experiment 2 we investigated ‘awkward grasping’ (using thumb and ring-finger; see Fig. 2). This grip type was previously used as an example of an unskilled action by Gonzalez et al. (2008). On the basis of a visual illusory effect on this kind of grasping, these authors concluded that unskilled actions are likely to be controlled by the ventral pathway instead of the dorsal pathway. In our experiment we instead used Garner-Interference as the indicator of the processing mode (Ganel & Goodale, 2003).

The results are almost identical to what we observed in Experiment 1. All aspects concerning the dual-task behavior were replicated, and again no Garner-Interference was observed. This suggests that awkward (or more general: unskilled) grasping is also not controlled by a qualitatively different processing stream than normal grasping is. Again, this interpretation contrasts the one advanced by Gonzalez et al. (2008).

## 8. Experiment 3

Experiments 1 and 2 were PRP experiments, where the particular grasping task was implemented as Task 2. The reason for this was

that we expected Garner-Interference, as the used grasping types were suggested relying on ventral information (Gonzalez, Ganel et al., 2006; Gonzalez, Goodale, et al., 2006; Gonzalez et al., 2008). This would have allowed assessing whether the additive interaction of Garner-Interference and SOA, as observed for perceptual judgment tasks, would replicate in action contexts. Yet, no Garner-Interference was observed so far, and this prompts the question if perhaps the dual-task PRP situation may have blurred this effect in grasping tasks. To exclude this possibility, we ran Experiment 3 as a single-task experiment where participants used again the awkward grip.

## 8.1. Method

### 8.1.1. Participants

Sixteen new undergraduates from Dortmund University of Technology (1 male, mean age = 23;9 years) participated in return of course credit. All participants were right-handed (by self-report).

### 8.1.2. Design, apparatus, stimuli, procedure, and data treatment and analyses

In this experiment, participants worked only on a grasping task and used the awkward grip of Experiment 2 to grasp the stimulus blocks (see Figure 2). Every trial began with a short warning click, and after 800 ms or 1200 ms (randomly varied) the shutter glasses opened and provided view of the stimulus block. Data analysis was done by means of ANOVA with condition (baseline vs. filtering) as a repeated measure. 3.1% of the trials were excluded as outliers.

## 8.2. Results and discussion

Mean RTs were 316 ms and 311 ms and mean MTs were 634 ms and 639 ms for baseline and filtering conditions, respectively. Neither on RTs;  $F(1,15)=0.35$ ,  $p=.56$ , partial  $\eta^2=.02$ ; nor on MTs;  $F(1,15)=0.24$ ,  $p=.63$ , partial  $\eta^2=.02$ ; had condition a significant effect. Mean error percentages were 1.56 and 1.48 for baseline and filtering blocks. This difference was not significant;  $F(1, 15)=0.78$ ,  $p=.79$ , partial  $\eta^2=.01$ .

In sum, these results suggest that also under single-task conditions no Garner-Interference is observed for awkward grasping, again pointing to a dorsal mode of processing (Ganel & Goodale, 2003). As such, the claims made from Experiments 1 and 2 are further strengthened.

## 9. Experiment 4

So far we are left with two rather disappointing results. Neither left-handed grasping (Experiment 1) nor 'awkward grasping' (Experiments 2 and 3) showed any signs of Garner-Interference. This outcome would actually be predicted assuming that the involved planning mechanisms and processes were able to ignore the task-irrelevant variation of the stimuli' length. Of importance, however, this ability has been ascribed to dorsal processing (Ganel & Goodale, 2003) and we thus must conclude that both left-handed and awkward grasping are controlled by this very mode. Taking this interpretation for serious, our results (where we used the Garner-Interference as the indicator) show exactly the opposite than those reported by Gonzalez, Ganel, et al. (2006) and Gonzalez et al. (2008), using the effect of visual illusions on grasping as the indicator.

Before we discuss the implications of these results we wish to point out three issues. First, our interpretations so far are based on three null-findings, what immediately raises the question of whether we had employed enough statistical power. We suspect this an unlikely problem to our study (actually, the mean RT2 differences between baseline and filtering conditions were very small), but concur that a higher-powered experiment would strengthen

our interpretation. A second and related issue is that we have thus far not included any control condition to test whether Garner-Interference can be observed in a typical ventral task. If the same participants would produce Garner-Interference in such a task, but at the same time not in a grasping movement under investigation here, this would be compelling evidence for our conclusions. Thirdly, even though having shown the desired effect in an earlier study (Gonzalez et al., 2008) the awkward grip may not have been unskilled enough and has thus escaped ventral control. Hence the use of a different unskilled grasping task appears desirable.

In Experiment 4 we addressed all of these three points: to enlarge the power of the experiment we used 32 (instead of 16) participants, all participants took part in a grasping task and in a ventral perceptual judgment (control) task, and they grasped the target stimuli using a realistic tool (pliers). In light of the results from Experiments 1 to 3 we (1) expected to replicate the dual-task characteristics, and (2) more importantly, we expected the occurrence of Garner-Interference in the perceptual task, but not in the tool grasping task.

## 9.1. Method

### 9.1.1. Participants

Thirty-two new undergraduates from Dortmund University of Technology (6 male, mean age = 24;6 years) participated in return of course credit. All participants were right-handed (by self-report) and had normal or corrected-to-normal vision.

### 9.1.2. Design, apparatus, and stimuli

Each participant was tested in two sessions of a PRP experiment lasting between 60 and 90 min. Task 2 was a tool grasping task in one session, in the other session Task 2 was a perceptual judgment task. Task 1 was always the binary tone classification task as described in Experiment 1, and the responses to this task were given with the left hand. With tool grasping as Task 2, participants used pliers with their right hand. The home-button was depressed with the tip of the pliers (we mounted a small plate of 3 cm × 3 cm on the home-button to facilitate this), and the participants were asked to precisely grasp the stimulus blocks with these pliers (see Fig. 4). The perceptual judgment task was modeled after Ganel and Goodale (2003). Here, participants were asked to judge the stimulus blocks' width and to respond with a right-hand key press accordingly. This task has been shown to reliably produce Garner-Interference in single-task settings (Ganel & Goodale, 2003), but also in dual-task settings (Janczyk & Kunde, 2010, Experiment 1; Kunde, Landgraf, et al., 2007). RT2 in this task was measured from the glasses opening until the right-hand key press was given.

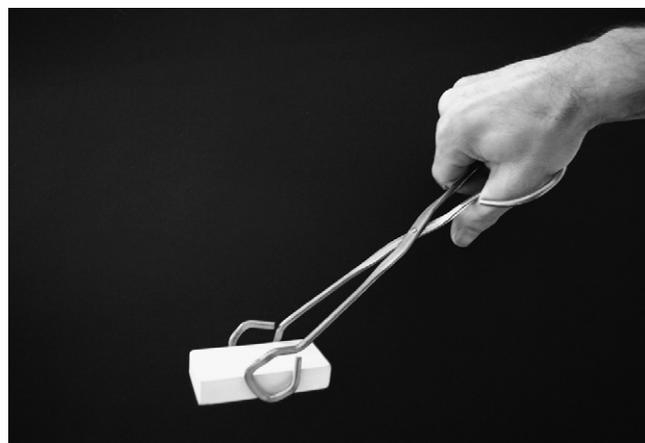
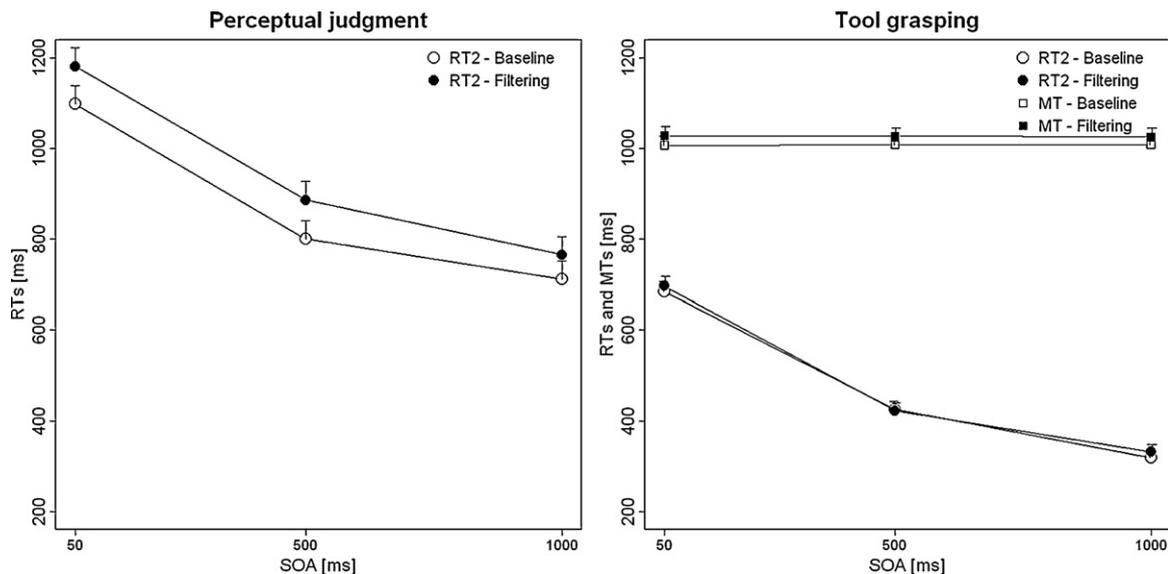


Fig. 4. Illustration of the tool grasping task used in Experiment 4.



**Fig. 5.** Mean response times (RTs) in milliseconds for the perceptual judgment task of Experiment 4 (left panel) and mean RTs and movement times (MTs) in milliseconds for the tool grasping task of Experiment 4 (right panel) as a function of SOA (stimulus onset asynchrony) and condition.

In all other aspects the experiment was similar to Experiments 1 and 2.

### 9.1.3. Procedure

Procedural details were for the most parts as described in Experiment 1. In both sessions participants were given the appropriate written instructions and performed a practice block before the four experimental blocks were administered.

The order of the tool grasping and the perceptual judgment task as Task 2 (2), of experimental blocks (4), and the stimulus-response-mapping of Task 1 (2) were counterbalanced across participants.

### 9.1.4. Data treatment and analyses

Analyses were done by means of analysis of variance (ANOVA) with the factors type of Task 2 (tool grasping vs. perceptual judgment), condition (baseline vs. filtering), and SOA (50 ms vs. 500 ms vs. 1000 ms) as repeated measures (Greenhouse-Geisser corrections were applied where necessary).

With tool grasping as Task 2, 3.7% and 4.0% of the trials in Tasks 1 and 2 were excluded as outliers; the corresponding values for perceptual judgment as Task 2 are 3.3% and 3.0%

## 9.2. Results

### 9.2.1. RT and MT analyses

Mean RTs and MTs in Task 2 are visualized in Fig. 5, separately for the perceptual judgment task (left panel) and the tool grasping task (right panel). In general, RT2 in the perceptual judgment task were significantly longer than in the tool grasping task;  $F(1,31)=138.92$ ,  $p<.01$ , partial  $\eta^2=.82$ ; and showed a decrease with an increasing SOA—the PRP effect;  $F(2,62)=320.77$ ,  $p<.01$ , partial  $\eta^2=.91$ ,  $\epsilon=.61$ . This decrease was roughly the same for both possible Tasks 2, yielding a non-significant interaction of SOA and Task 2 type<sup>3</sup>;  $F(2,62)=2.03$ ,  $p=.16$ , partial  $\eta^2=.06$ ,  $\epsilon=.61$ ; and it was also the same for baseline and filtering conditions, resulting in

<sup>3</sup> When this analysis was applied to log-transformed RTs, this interaction effect reached significance, indicating differences in the PRP effect between both tasks. As differences in PRP effects are difficult to interpret, and this interaction is not of theoretical interest for the present purposes we refrain from going into detail here.

a non-significant interaction of SOA and condition;  $F(2,62)=1.11$ ,  $p=.34$ , partial  $\eta^2=.03$ .

Of most importance for the present purposes was the significant main effect of condition with longer RTs in filtering conditions than in baseline conditions, indicating the occurrence of Garner-Interference;  $F(1,31)=6.82$ ,  $p=.01$ , partial  $\eta^2=.18$ . However, this main effect was further modulated by the type of Task 2: the size of Garner-Interference was about 100 ms in the perceptual judgment task, at the same time Garner-Interference was nearly absent in the tool grasping task. Accordingly, the interaction of condition and type of Task 2 was significant;  $F(1,31)=7.94$ ,  $p<.01$ , partial  $\eta^2=.20$ . The three-way interaction of SOA  $\times$  condition  $\times$  Task 2 type did not reach significance;  $F(2,62)=1.29$ ,  $p=.28$ , partial  $\eta^2=.04$ . MTs were higher than those observed in Experiments 1–3 and they varied between 1007 ms and 1028 ms. No effect reached significance in the respective ANOVA; SOA:  $F(2,62)<0.01$ ,  $p>.99$ , partial  $\eta^2<.01$ ; condition:  $F(1,31)=2.20$ ,  $p=.15$ , partial  $\eta^2=.07$ ; interaction SOA condition:  $F(2,62)=0.02$ ,  $p=.98$ , partial  $\eta^2<.01$ .

Mean RTs in Task 1 (see Table 1) were higher with the perceptual judgment task as Task 2 compared to tool grasping as Task 2;  $F(1,31)=27.44$ ,  $p<.01$ , partial  $\eta^2=.47$ . RT1 were numerically slightly smaller in the baseline conditions than in the filtering conditions, but the corresponding effect did only approach significance;  $F(1,31)=3.77$ ,  $p=.06$ , partial  $\eta^2=.11$ . There was a reliable effect of SOA on RT1;  $F(2,62)=4.97$ ,  $p=.03$ , partial  $\eta^2=.14$ ,  $\epsilon=.57$ ; but this effect was modulated by a significant interaction of SOA and type of Task 2;  $F(2,62)=10.46$ ,  $p<.01$ , partial  $\eta^2=.25$ ,  $\epsilon=.61$ : whereas RT1 again increased with an increasing SOA with tool grasping as Task 2, RT1 remained almost constant with the perceptual judgment task as Task 2. No other effect was significant.

### 9.2.2. Error analyses

Mean error percentages are presented in Table 2 and the detailed statistics are summarized in Table 3. Task 1 error rates were comparable to those in Experiments 1 and 2, and they decreased significantly with an increasing SOA. Task 2 error rates were in general higher than in the previous Experiments 1 and 2. Also, they were significantly higher with the perceptual judgment task as Task 2. Of importance, they were also significantly higher in filtering conditions than in baseline conditions, but this was only true when perceptual judgment was Task 2 (resulting in a significant interaction of condition and type of Task 2).

### 9.3. Discussion

Experiments 1–3 have consistently shown that left-handed grasping and awkward grasping (as an instance of an unskilled movement) are not susceptible to Garner-Interference. According to the logic of Ganel and Goodale (2003) this suggests a dorsal processing mode, and at the same time contradicts recent proposals that these actions escape dorsal processing and are under ventral control (Gonzalez, Ganel, et al., 2006; Gonzalez, Goodale, et al., 2006; Gonzalez et al., 2008). In Experiment 4 we investigated another variant of a likely unskilled movement, and the participants were asked to grasp the stimuli with a realistic tool, namely pliers. This tool grasping task was implemented as Task 2 in a PRP experiment, and in addition the participants were tested in a second session where Task 2 was a perceptual judgment task. With this, presumably typical ventral, task Garner-Interference has repeatedly been shown (Ganel & Goodale, 2003; Janczyk & Kunde, 2010; Kunde, Landgraf, et al., 2007) and it thus served as a control condition in Experiment 4.

The results are quickly summarized, as they are very similar to those reported for Experiments 1 and 2. First, for both tasks (the tool grasping and the perceptual judgment task) we observed the typical dual-task behavior and both tasks appear to recruit central resources (to the same degree). Second, and more importantly, large Garner-Interference was found for the perceptual judgment task, and Garner-Interference combined additively with SOA as has been reported previously (Janczyk & Kunde, 2010; Kunde, Landgraf, et al., 2007). Third, and most important, despite doubling the sample size and successfully finding Garner-Interference in the perceptual judgment task with the same participants, no Garner-Interference was found in the tool grasping task. This result nicely corroborates the results of our previous Experiments 1–3 and reinforces the claim that neither left-handed nor unskilled grasping movements are controlled by a different processing stream than normal, right-handed grasping is.

## 10. General discussion

The present study was conducted to test whether left-handed and/or unskilled grasping relies on perceptual information from the ventral pathway instead of being controlled by the dorsal pathway (Gonzalez, Ganel, et al., 2006; Gonzalez, Goodale, et al., 2006; Gonzalez et al., 2008). Contrary to these earlier studies we used Garner-Interference as the behavioral indicator of the underlying processing mode (Ganel & Goodale, 2003). We ran three dual-task PRP experiments and one single-task experiment where different grasping tasks were administered (as Task 2 in the PRP experiments): in Experiment 1 the participants used a left-handed precision grip, in Experiments 2 and 3 they used an awkward grip with their right hand, and in Experiment 4 they used pliers (handled by their right hand) to grasp small wooden blocks. The results can be summarized quickly since they all converge in the same conclusion: never did we find Garner-Interference across these three grasping tasks, and – following the reasoning of Ganel and Goodale (2003) – we need to conclude that they all were mediated by the dorsal pathway instead of relying on perceptual information provided by the ventral pathway. Obviously this contrasts with the proposals by Gonzalez, Ganel, et al. (2006) and Gonzalez et al. (2008) and highlights the importance of independent evidence and the use of varying methods. In light of the controversial debate around the illusory effects on action and perception, we consider our results clear-cut and suggest that there is no need for distinguishing between two classes of actions: one guided by a different processing stream than the other. In terms of theory building this

would also be good news as it means a step (back) towards parsimony.

### 10.1. Illusory effects revisited

As mentioned above several studies have reported comparable effects of visual illusions on perception and action (e.g., Franz et al., 2000, 2003; Pavani et al., 1999). Proponents of the Action-Perception model tried to reconcile these findings with their model by arguing that these studies have used intrusive devices to measure grip aperture, such that participants performed an awkward and unskilled movement. In consequence, grasping would have been guided by the ventral stream and therefore would – unsurprisingly – yield the same results as a typical perceptual task (e.g., Goodale, 2008). However, this argument relies on the one study by Gonzalez et al. (2008) which did not test this notion directly. In a direct test, contrasting the supposedly intrusive devices with non-intrusive devices, Franz, Hesse, and Kollath (2009) found equal illusion effects with both methods, thereby showing that the counterargument of Goodale (2008) is not valid. This result is corroborated and generalized by the present study using Garner-Interference as the behavioral marker.

### 10.2. The dual task behavior of left-hand and unskilled grasping movements

In addition our results allow concluding that unskilled and left-handed grasping is subject to massive dual-task interference, by demonstrating a PRP effect across all three PRP experiments. This is less surprising since we have shown elsewhere that even right-handed precision grasping is subject to dual-task interference (Janczyk & Kunde, 2010; Kunde, Landgraf, et al., 2007). Still, our results may be informative regarding the cognitive costs of tool use. An ANOVA comparing the PRP effects (calculated as the difference of RT2 between the SOAs of 50 ms and 1000 ms) across the three PRP experiments yielded a significant main effect of experiment; ( $F(2,61) = 666.81, p < .01, \text{partial } \eta^2 = .33$ ). Post-hoc Scheffé tests, however, localized the source for this effect in the fact that the PRP effect in Experiment 1 (531 ms) was significantly larger than in Experiment 2 (317 ms) and Experiment 4 (367 ms). The latter two PRP effects were not significantly different. Thus, in terms of cognitive costs, grasping with a tool seems to not differ from other unskilled actions. It may even be that the higher PRP effect for left-handed grasping (Experiment 1) was inflated, since RT1 was the highest in this experiment, too. Note that we need to be cautious when comparing PRP effects across experiments (or experimental conditions). In general, PRP effects are difficult to interpret, since the size of PRP effects is, for example, a function of RT1 (see, e.g., Lien, McCann, Ruthruff, & Proctor, 2005). Clearly, further and more sophisticated research using a within-subject manipulation of the grasping conditions and including a right-hand precision grip control condition is necessary to more thoroughly assess the dual-task costs of different grasping actions.

Interestingly there seems to be a consistent (but non-significant) trend of condition on RT1. Such a (crosstalk-) effect of Task 2 on Task 1 would not be compatible with strictly serial bottleneck models like the one advanced by Pashler (1994). To accommodate such findings Hommel (1998) and Lien and Proctor (2002) suggested to divide the central stage into two sub-stages: (1) a first stage of stimulus-response translation that can proceed in parallel to other stages and – when two such stages overlap – is the source of mutual interference (or facilitation) between tasks, and (2) a second bottleneck stage of final response selection.

We also replicated Garner-Interference in Experiment 4 when a perceptual judgment was used as Task 2. Comparable to previous reports (Janczyk & Kunde, 2010; Kunde, Landgraf, et al., 2007)

Garner-Interference combined additively with the factor SOA suggesting – according to the central bottleneck model and the PRP logic (Pashler, 1994; Pashler & Johnston, 1998; Appendix A) – an implication of central mechanisms, although intuitively Garner-Interference comes across as a perceptual phenomenon.

### 10.3. Conclusions

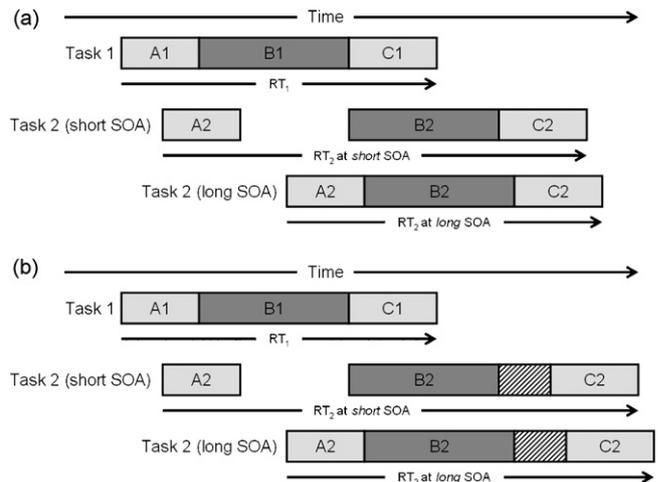
The present study tested two pieces of results related to the Action–Perception model (Milner & Goodale, 2006) for their mutual consistency: left-handed and unskilled grasping should rely on perceptual information from the ventral stream (Gonzalez, Ganel, et al., 2006; Gonzalez, Goodale, et al., 2006; Gonzalez et al., 2008), and the ventral stream should be susceptible to Garner-Interference (Ganel & Goodale, 2003). Across our four experiments never did we observe Garner-Interference for the grasping movements in question. As such, our study revealed an inconsistency in theorizing related to the Action–Perception model, and we suggest that left-handed and unskilled grasps are controlled by similar mechanisms as natural (right-handed) grasping is. Thus there is no need to distinguish several classes of visually guided (grasping) actions, which are controlled by different processing streams. It might be helpful to think about a less strong interpretation of the Action–Perception model, as this model is basically a neuroanatomical and neuropsychological theory. Both the visual illusion and the Garner-Interference arguments are derived from characteristics attributed to both visual pathways. Of course, our results do not question such interpretation: the core assertion of the Action–Perception model (the different purposes of both streams) may still be valid, even if such assumed characteristics turn out being wrong.

Our interpretation of the results, however, has also implications for applied research concerning the question of what characteristics of natural actions generalize to transformed and other artificial movements (Kunde, Müssele, et al., 2007). In particular, the characteristics of movements using virtual tools like a computer-mouse or other input devices might be quite similar to natural actions, a topic that should be investigated in future research.

### Appendix A. The central bottleneck model and the PRP paradigm

The psychological refractory period (PRP) paradigm is a dual-task paradigm allowing for rigorous control of the temporal succession of two stimuli. Because usually two different tasks are to be performed in response to these stimuli the amount of task overlap can be manipulated by the experimenter.

In a typical PRP experiment two tasks (Task 1 and Task 2) have to be performed in each trial and in rapid succession. Each task requires its own response (R1 and R2) to the corresponding imperative stimulus (S1 and S2). S1 and S2 are separated by a time interval referred to as the stimulus onset asynchrony (SOA). The SOA is experimentally manipulated and typically short and long intervals are used within an experiment, e.g., 50 ms and 1000 ms. The common finding is that RT2 (the response time in Task 2) decreases with an increasing SOA (the PRP effect), while RT1 (the response time in Task 1) is largely unaffected by the SOA manipulation. This pattern is quite robust and has been found with a variety of tasks and even if different stimulus and response modalities are employed (see Pashler, 1994; Pashler & Johnston, 1998, for overviews). Several accounts for the PRP effect were advanced, but the most widely accepted is the central (or response selection) bottleneck model first proposed by Welford (1952) and later formalized by Pashler (1994; Pashler & Johnston, 1998).



**Fig. A.1.** Illustration of a PRP experiment assuming a structural central bottleneck: (a) processing of Tasks 1 and 2 without experimental manipulations in addition to SOA, and (b) processing of Task 1 and 2 with a manipulation implemented in the central stage of Task 2. (A = pre-central stage, B = central stage, C = post-central stage; for further explanations please see Appendix A).

According to this model the processing of each task can be subdivided into at least three stages (for the following, please see Fig. A.1a in this Appendix): a pre-central perceptual stage (A), a central response selection stage (B), and a post-central motor stage (C). The crucial assumption is that stages A and C can be processed in parallel to other stages, while at any time only one stage B can be processed, thus constituting a processing bottleneck. With a short SOA the perceptual stage of Task 2 (A2) finishes before the central bottleneck has been released from the central stage of Task 1 (B1). Thus, Task 2 processing must be deferred yielding a longer RT2. In contrast, with a long enough SOA, stage A2 likely finishes only after the bottleneck has been released from Task 1, and thus Task 2 processing can continue without any deferment. A further prediction from this model is that any manipulation implemented in Task 2 that affects a central (or also post-central) stage adds the same amount of time to RT2 across all SOA levels. In this case the respective manipulation and the factor SOA combine additively. This situation is illustrated in Fig. A.1b.

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