Interference in skilled and unskilled grasping

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Abstract

Following the primary visual cortex, the human visual information system subdivides into two separate cortical streams: a ventral stream to the inferior temporal cortex, and a dorsal stream to the posterior parietal cortex. In their influential Action-Perception Model David Milner and Melvyn Goodale attributed to these streams different purposes: the ventral stream should create the conscious percept of the environment, while the dorsal stream should plan and control visually guided (and target directed) actions, such as grasping. Crucially, to exploit dorsal processing vision of the target object must be available at the moment of movement initiation. In contrast, pantomiming and delayed grasping were assumed to rely on perceptual information provided by the ventral stream. Among other characteristics, processing within the dorsal stream has been described as automatic and effortless.

In recent years several predictions from this model were investigated and the model was extended in several ways. First, attempts were made to elucidate whether dorsal processing is indeed automatic or not – but the results are mixed at best. Some authors conclude positive, others negative. One study reported a large PRP effect for a dorsal grasping task – a well-known marker for a central capacity requirement. Secondly, it was suggested in various studies that also unskilled and left-handed grasping is under ventral control. However, these suggestions are to date solely based on a controversial behavioral indicator, namely the effect of visual illusions on action.

The purpose of the present work was twofold. In a first series of three experiments I sought to rule out two alternative explanations for the PRP effect in grasping. At the same time an alternative indicator for ventral processing was further established: Garner-Interference, the ventral stream's inability to efficiently ignore variations of task-irrelevant stimulus dimensions. Garner-Interference was then used to assess ventral contributions to left-handed and unskilled grasping in a second series of four experiments.

According to the results from these experiments, neither right-handed precision grasping (typically ascribed to the dorsal stream) nor other types of grasping can be construed as automatic, but do interfere even with simple choice-reaction tasks. Additionally, no signs of Garner-Interference were observed across all employed grasps. This contrasts with recent reports from studies using visual illusory effects as the marker for ventral contributions.

Implications of these findings for dual-task research and for the Action-Perception Model are discussed. While the general tenet of this model is not questioned by my results, they nevertheless pose new constraints on its further development.

1 Introduction

It is fascinating how precise and skillfully humans use their hands to grasp, point at, reach, and manipulate objects – be it with their hands only or even using tools. Despite the superficial easiness, the underlying processes and mechanisms of this ability are quite complex. In general, grasping is – at least for healthy people – intriguably linked to vision (Jeannerod, 1986, p. 41):

> "Visually directed action implies continuous transformation of incoming visual stimuli into motor commands. At the same time, action generates new visual stimuli which may be used as control signals to guide execution of the commands."

This interplay of action and perception has received a vast amount of attention in Cognitive Psychology, and the present work aims at contributing to our understanding of this issue by analyzing two aspects of grasping movements: their susceptibility to dual-task interference and their assumed underlying planning mechanisms. The present chapter thus continues with brief overviews of kinematic characteristics of grasping (Section 1.1) and the human visual processing system (Section 1.2) inasmuch as they are of relevance to the present work. As will be seen, the visual system can be divided into two streams on various levels and early accounts for these dichotomies will be reviewed in Section 1.3. Finally, I will give the reader an orientation about the structure of the present work (Section 1.4).

1.1 Grasping objects

Object-directed hand movements are essential to our daily survival, both in everyday situations and also in many working contexts. We use our hands to manipulate and grasp objects, but also for communicative reasons, such as pointing at objects. In addition, the exact grip-type clearly depends on the intended activity with the to-be-grasped object. For example, Napier (1993) drew a distinction between a *power grip* and a *precision grip* (see Figure 1.1): while in the former, all fingers are coordinated in a synergistic way, the precision grip requires independent organization of all fingers in order to grasp an object between the thumb and the index-finger.


(a)

(b)

Figure 1.1: Illustration of two different grip types: (a) a power grip between the thumb and all fingers, and (b) a precision grip between the thumb and the index-finger.

Such a precision grip begins to evolve far before the fingers hit the target object. Indeed, the hand appears to anticipate the final position from the very onset of the movement, beginning with a progressive opening of the grip and followed by a gradual closure resulting in the final grasp position (e.g., Castiello, 2005; Napier, 1993; Smeets & Brenner, 1999). An important kinematic marker is the the widest in-flight opening between the thumb and the index-finger, the *maximum grip aperture (MGA)*. The MGA is typically observed after about 60-70% of the whole movement and is linearly related to the actual size of the target. Thus, it is often considered a valid dependent variable indicating the precision of a grasping movement (but see Castiello, 2005). In addition to the target's size other characteristics such as weight and surface structure determine the exact kinematics of a movement (for a review, see Smeets & Brenner, 1999).

1.2 The human visual information processing system

Vision begins as light rays arive at our eyes and eventually hit the *retina* (for an overview, see Kaneko, 1979). The retina itself is a small neural tissue consisting of receptors (*rods* and *cones*) that forward their excitation via *horizontal*, *bipolar*, and *amacrine cells* into the *retinal ganglion cells*. The axons of these retinal ganglion cells form the *optic nerve* which leaves the eye ball at the *optic disc* (Kaneko, 1979; Levine, 2000; Pinel, 2003). Both optic nerves intersect in the *optic chiasm*, where the nerves divide into the *optic tracts* in a particular way: the retinal ganglion cells' axons starting off the *nasal retina* (i.e., the part of the retina closest to the nose), continue their way into the contralateral brain hemisphere. In contrast, those axons beginning in the *temporal retina* (i.e., the part of the retina towards the temples) continue their way within the ipsilateral hemisphere (e.g., Levine, 2000; Pinel, 2003; Rodieck, 1979). As a consequence, each hemisphere receives input from the opposite side of the visual world.

Six regions receive projections from the retinal ganglion cells (Rodieck, 1979), two of which are well investigated and of some importance to the present work: a smaller portion of the optic tracts projects to the *superior colliculi* (see below), and a larger part projects into the *dorsal lateral geniculate nucleus* (LGN_d) of the *thalamus*. The LGN_d is a six-layer structure, and each layer receives input from only one eye: layers 1,4, and 6 from the contralateral eye, and layers 2, 3, and 5 from the ipsilateral eye. Thus, both eyes' information remains uncombined at this point. Another feature of the LGN_d is that layers 1 and 2 consist of large cells (*magnocellular*), whereas layers 3-6 are made of small cells (*parvocellular*). Noteworthy, this distinction can be traced back to the retina, where two types of retinal ganglion cells can be distinguished: the relatively large type A cells project into the magnocellular LGN_d layers, while the smaller type B cells terminate in the parvocellular LGN_d layers (Leventhal, Rodieck & Dreher, 1981). According to Livingston and Hubel (1988) both layer-types differ in responsiveness regarding color, temporal resolution, contrast sensitivity, and acuity: a color-blind but fast and high contrast sensitive magnocellular system with low spatial resolution on the one hand; on the other hand a slow but color-selective parvocellular system with low contrast sensitivity and high spatial resolution. Similarly, Schiller, Logothetis and Charles (1990) have shown that parvocellular lesions in monkeys detoriate perception of color and depth, while magnocellular lesions impair motion detection.

Located in the *occipital lobe*, the *primary visual cortex* ($V1$, or *striate cortex*) is the first cortical area receiving visual input from the LGN_d. $V1$ consists of six layers, some of which are subdivided into smaller parts. The magno- and parvocellular distinction within the LGN_d is first maintained in $V1$: magnocellular layers mainly project into $V1$ layers $4C\alpha$ and 6, whereas the parvocellular layers project into $V1$ layers $4C\beta$ and $4A$ (e.g., Levine, 2000; Merigan & Maunsell, 1993; Tootell, Silverman, Hamilton, DeValois & Switkes, 1988). Particularly important for the present work, projections from $V1$ into higher (visual) areas appear to be subdivided into two cortical streams (see Figure 1.2) that have already been described by Flechsig (1896, cited in Ungerleider & Mishkin, 1982): a *ventral stream* projects (mainly via areas $V2$, $V3$, and $V4$) into the *inferior temporal cortex (ITC).* In contrast, a *dorsal stream* continues into the *posterior parietal cortex (PPC)* (mainly via areas $V2$, $V3A$, MT (= *mediotemporal cortex*), and MST (=*medial superiortemporal cortex*)). Compared to the ITC, the PPC receives more input from the contralateral visual field, and also more peripheral information (Ungerleider & Mishkin, 1982). Note that the separation of these two streams is far from being perfect with various cross-connections between them (for a more detailed neuroanatomical discussion, see Merigan and Maunsell (1993), Milner and Goodale (1995, 2006), Ungerleider and Haxby (1994), or Ungerleider and Mishkin (1982)). It has been suggested that the dorsal and the ventral stream are the cortical continuations of the magno- and the parvocellular pathways (Livingston & Hubel, 1988). However, it appears as if both streams receive parvo- and magnocellular input, although most of the dorsal stream's input is magnocellular (Merigan & Maunsell, 1993). While the dorsal-ventral stream distinction has originally been based on work with macaque monkeys, it seems to apply to the human cortex as well (Ungerleider & Haxby, 1994). A detailed comparison of the human and the macaque cortex is given by, e.g., Tootell, Tsao and Vanduffel (2003).

Thus far I have described the *retinogeniculate pathway* of visual processing. As is illustrated in Figure 1.2, the PPC also receives input via the phylogenetically older *retinotectal pathway.* The *pulvinar*, a complex thalamus nucleus, receives input from the superior colliculi and, to a smaller degree, directly from the retina. Distinct areas of the pulvinar then project into both the dorsal and the ventral stream. However, the ITC lacks responsitivity following complete $V1$ lesions, rendering the functional role of the pulvinar-ITC projections somewhat unclear. In contrast, the PPC still receives input, presumably via this retinotectal pathway (Robinson & McClurkin, 1989; Ro, 2008).

1.3 Early theories about 'two visual systems'

As sketched in the previous section, a (subcortical) retinotectal pathway can be distinguished from a retinogeniculate pathway, and after $V1$ two cortical streams emerge: a dorsal stream to the PPC, and a ventral stream to the ITC. Obviously, such anatomical segregations suggest functional segregations, too. Beginning in the 1960ies a number of functional dichotomies were advanced and mapped onto these different neural streams.

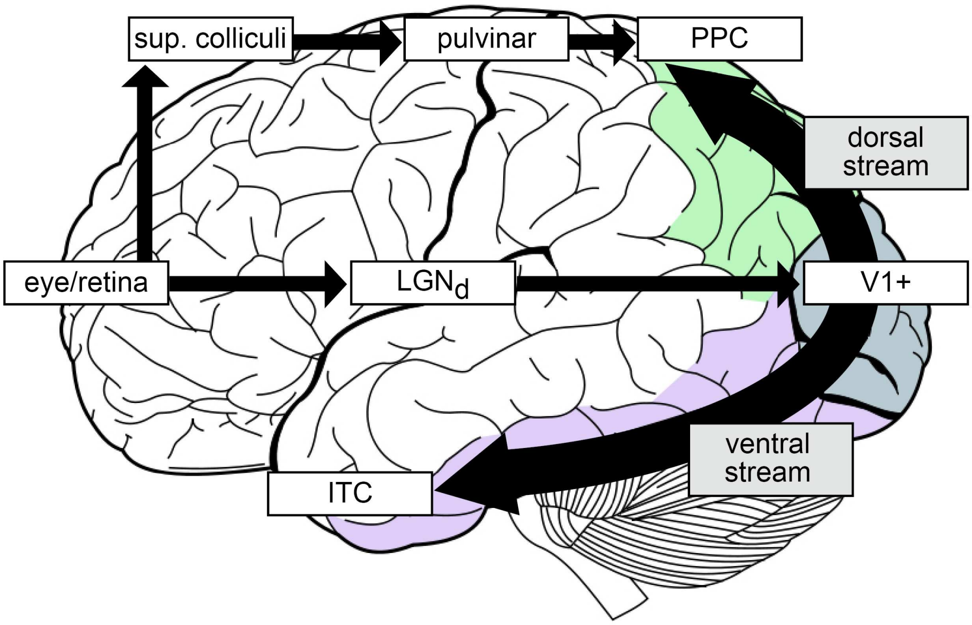

Figure 1.2: A simplified version of the streams for visual processing: both the posterior parietal cortex and the inferior temporal cortex receive input starting off the primary visual cortex. In addition to these cortical routes, the posterior parietal cortex is fed subcortically via the superior colliculi and the pulvinar nucleus of the thalamus. (*Note:* sup. colliculi = superior colliculi; LGN_d = laterale geniculatum nucleus dorsal; $V1+$ = primary visual cortex and higher regions; ITC = inferior temporal cortex; PPC = posterior parietal cortex)

For example, Trevarthen (1968) made a distinction between *focal vision* (for details in small areas of space) and *ambient vision* (to determine space around the body on the whole). According to this theory, ambient vision would be driven by the retinotectal pathway and serves for the guidance of whole-body movements. In contrast, the retinogeniculate pathway underlies focal vision, which in turn directs finer motor acts, such as a hand’s grasping movement. A different hypothesis was put forward by Schneider (1969), who ascribed to the retinotectal pathway the localization of objects ("Where?"), but to the retinogeniculate pathway the identification of these same objects ("What?"). Both theories, however, place their emphasis on different roles of the retinotectal and the retinogeniculate pathway.

The perhaps most influential hypothesis on ’two visual systems’ was published by Ungerleider and Mishkin (1982, see also Ungerleider & Haxby, 1994). These authors drew on the functional "What?" *vs.* "Where?" distinction (Schneider, 1969), but mapped these two functions on the ventral and the dorsal stream, respectively, thus exclusively on cortical regions. In a series of studies with macaque monkeys Ungerleider, Mishkin and colleagues have shown that lesions of the *ITC* lead to impairments in visual-discrimination tasks, while lesions of the *PPC* result in impaired performance in landmark tasks. Reviewing the available evidence from a number of studies, it was concluded (Ungerleider & Mishkin, 1982, p. 579)

> ”...that appreciation of an object’s qualities and of its spatial location depends on the processing of different kinds of visual information in the inferior temporal and posterior parietal cortex, respectively.”

A similar double dissociation has further been reported in humans. For example, Newcombe, Ratcliff and Damasio (1987) reported on two case studies with impaired visual recognition or visuospatial performance following occipitotemporal or occipitoparietal lesions, respectively (according to a postmortem examination). Such observations led Ungerleider and Haxby (1994) to suggest that in humans, too, the ventral stream acts as a ”What?”-stream, while the dorsal stream can be interpreted as a ”Where?”-stream. Tentatively, such an interpretation does also make sense in light of more recent imaging studies. For example, area *MT*, a main input area for the dorsal stream, has been implicated in the detection of (pattern) motion (e.g., Born & Bradley, 2005; Grill-Spector & Malach, 2004). In contrast, object-selective areas have been identified within the ventral stream, among them the *fusiform face area (FFA)* and the *parahippocampal place area (PPA)* (Epstein & Kanwisher, 1998; Kanwisher, McDermott & Chun, 1997).

1.4 Organization of the present work

In the last two sections I have described the basic layout of the human visual processing system and some early theories on functional divisions of labor between distinctive processing streams – finishing with the proposal of a ”What?”- *vs.* a ”Where?”-stream by Ungerleider and Mishkin (1982) and Ungerleider and Haxby (1994). The evidence for this model has, however, been reinterpreted with a lasting effect by Goodale and Milner (1992) in their *Action-Perception Model*, and this model provides the theoretical basis for the present work. Hence I will review it in greater detail in the following Chapter 2. One central aspect of this present work relates to the dual-task behavior of various grasping movements. In particular, the majority of the here reported experiments is settled within the paradigm of the *psychological refractory period (PRP)*, which I will introduce in

Chapter 3. In Chapter 4 I will then sketch the empirical part more detailed, and will then present two series of experiments in Chapters 5 and 6, which are discussed comprehensively in Chapter 7.

> **Before moving on, let me point out two things:**
> First, the present study does not use neuroimaging techniques, and as a consequence I won't be able to make well-grounded comments about the underlying neural substrates for the empirical results that I will present later. The soon to-be-introduced terms 'vision for perception' and 'vision for action' on the one side, and 'ventral stream' and 'dorsal stream' on the other side, will thus be used in an interchangable way. By no means I do claim to make definite conclusions about the underlying neural systems. In other words: both pairs of terms are meant to refer to two different (cognitive) processing modes and their constraints and characteristics, rather than to specific neuroanatomical structures.
>
> The second point is that it is impossible to give an exhaustive review of the sheer enormity of studies that have been published in relation to the two theoretical frameworks underlying the present work, the Action-Perception Model and the PRP paradigm[1]. If anything, I attempt to provide the reader in the following two chapters with an overview of the present discussions and the most important theoretical positions.

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[1] According to the Scopus database, the paper by Goodale and Milner (1992) has been cited 1258 times, and even the study by Aglioti, DeSouza and Goodale (1995) has been cited 339 times. Regarding dual-task research, Pashler (1994) has already received 562 citations (queried on the 1st of June, 2010).

2 Milner and Goodale's Action-Perception Model

The proposal of a dorsal "Where?"-stream and a ventral "What?"-stream (Ungerleider & Mishkin, 1982; Ungerleider & Haxby, 1994), as introduced in Section 1.3, was criticized several years later by David Milner and Melvyn Goodale. In their very influential *Action-Perception Model* they argued that both streams do not differ with regard to the input they handle. Rather, both streams would process essentially the same input, but for different purposes (Goodale, 2008; Goodale & Humphrey, 1998; Goodale & Milner, 1992, 2004b; Milner & Goodale, 1995, 2006, 2008): the ventral stream constructs the conscious percepts from vision, and the dorsal stream as a planning and on-line control mechanism for visually guided actions.

I will start this chapter by describing the Action-Perception Model in Section 2.1, followed by a discussion of neuropsychological and behavioral evidence for this model (Sections 2.2 and 2.3). In Sections 2.4 and 2.5 I will analyze the empirical evidence for the claims that the dorsal stream only works in real-time and also automatic and without central capacity requirements. Finally, in Section 2.6 I will enter into the question of how to identify a dorsal or ventral processing mode by means of behavioral data.

2.1 A reinterpretation of the two (cortical) visual systems

What has vision evolved for? Likely, most people would answer: "Sight". In other words, vision allows us to "see" our current environment in order to, e.g., recognize objects. Yet, this answer may not be true for most animals. Indeed, it has been argued that the main purpose for vision in animals is to direct their movements through the environment (for overviews, see Goodale & Humphrey, 1998; Milner & Goodale, 1995, 2006). Early work by Ingle (1973, 1980) with re-wired frogs demonstrated that the visual system of frogs consists of relatively independent streams, each responsible for a particular class of behavior (e.g., snapping movements via the tectum (Ingle, 1973), or barrier avoidance via the pre-tectum (Ingle, 1980)). Conceivably, in higher mammals, and especially in humans, everyday affordances require more flexibility. This in turn suggests the involvement of the phylogenetically more recent cerebral cortex (Goodale & Humphrey, 1998; Milner & Goodale, 1995, 2006). Note that with the retinotectal pathway an example for a more ancient subcortical PPC input into the visual system still exists (see Section 1.2 and Figure 1.2).

Inspired by such considerations and additional findings from the patient D.F. (see Section 2.2.1 for more details), Goodale and Milner (1992)[1] argued that the two cortical visual streams do not differ with regard to the information they process. Rather they emphasized the underlying transformations these two streams perform on essentially the same input – but for different purposes. In short (more details are given below), it was suggested that the ventral stream processes *vision for perception* and the dorsal stream processes *vision for action*. The focus was thus shifted from the input to the output of both systems.

What are these different transformations necessary for either purpose, that have prompted the development of two cortical streams (for a more detailed discussion of the following paragraph see Milner and Goodale (1995, 2006) or Goodale and Milner (2004b))?

- **Vision for perception:**

  The ventral stream was proposed to create the *conscious percept* of our environment that allows us to initially store and later recognize objects. Further, these information may be used to imagine (or even plan) actions "offline", i.e., in the absence of any direct visual input.

  Logically, it is impossible to recognize something we have never encountered before. Hence, representations created by the ventral stream are to survive for a longer period of time, a property commonly understood as *memory*. Furthermore, an object's relations to its own environment are clearly of interest for the perceptual system: implicitly, we perceive the size or the location of objects relative to other objects. Goodale and Milner (2004b) illustrated this by arguing that we are not confused whether a movie is watched on a tiny TV set or on a large cinema screen. Put differently, to recognize objects, it does not greatly matter whether an object is a tiny bit smaller or larger on the retinal image, or whether it is viewed from an

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[1] These ideas were later extensively discussed in Milner and Goodale (1995, 2006) and, in a more popular scientific, though accessible, way in Goodale and Milner (2004b).

orientation different than at the first encounter. As a consequence, for perception it does make sense to code spatial locations in *relative, allocentric coordinates.*

- **Vision for action:**

  In contrast, the dorsal stream provides the *direct, fast, and unconscious* transformations required for planning and controlling visually guided actions.

  Rarely if ever do humans stay in a static relationship with their environment. Thus, if acting upon an object, it makes little sense to base these movements on stored information. Rather, when programming a movement, the system is well advised to only take into account the *real-time* and just now present information. Given that the spatial relationship to the object changes rapidly, there is no need to store these programs (or spatial coordinates), as they are of little later use. In fact, it would overburden the cognitive system if all possible motor plans would be stored during life. Additionally, precise movements require knowledge about the exact location of an object in relation to the actor. It is thus essential to code spatial locations in *absolute, egocentric coordinates.*

It is clear from this brief description that both streams presumably differ on several (cognitive) dimensions, and Table 2.1 summarizes the most important ones (for more details and further elaborations see Milner and Goodale (1995, 2006) or Norman (2002)).

Table 2.1: A comparison of the dorsal vision for action and the ventral vision for perception system on selected (cognitive) dimensions.

	vision for perception	**vision for action**
neural system	ventral stream to ITC	dorsal stream to PPC
spatial coordinates	relative, allocentric	absolute, egocentric
memory access	access to LTM representations	only real-time processing
resource requirement	resource demanding, conscious	fast, automatic, unconscious
processing mode	holistic	analytic

In the remainder of this Chapter I will discuss and evaluate the available empirical evidence for these distinctions. Section 2.2 is dedicated to the neuropsychological evidence that has been cited to ascribe the action role to the dorsal stream and the perception role to the ventral stream. Historically, the neurological conditions of visual agnosia and optic ataxia (see Section 2.2.1) have largely been the basis for the Action-Perception Model. In Sections 2.3 and 2.4 I will then address the distinction of ego- *vs.* allocentric coding of spatial coordinates and the real-time view of dorsal processing: in my opinion these issues are highly important for the Action-Perception Model (and as a consequence for our understanding of action control), as unequivocal evidence from studies with healthy people would clearly allow a better assessment of the Action-Perception Model. The last two properties listed in Table 2.1 are not so well investigated, but are most important to the empirical part of the present work. I will discuss the few available studies directly addressing these issues in Sections 2.5 and 2.6. To anticipate the outcome of the following sections: for the most parts the available evidence appears to forbid a definite answer at the present state.

2.2 Neuropsychological evidence for the Action-Perception Model

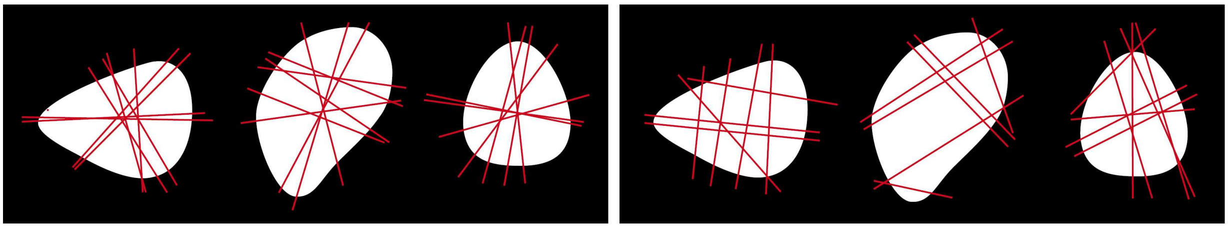
Much of the initial evidence for the Action-Perception Model came from neuropsychology. For example, patients with $V1$ lesions sometimes show motor responses to visual stimuli about which they cannot give a conscious report. This condition has been termed *blindsight* or *cortical blindness* (Weiskrantz, 1986). At first glance quite a puzzling phenomenon it has been suggested that, in the absence of $V1$ input, the retinotectal pathway still provides the PPC with (admittedly impoverished) input, on which the residual motor abilities are based. Not surprisingly, alternative explanations have been put forward, too. An example is the existence of a few, but still functioning, $V1$ islands (Wessinger, Fendrich & Gazzaniga, 1997).

2.2.1 Visual agnosia vs. optic ataxia

Among the most intriguing support for the Action-Perception Model are the neurological conditions of *visual agnosia* and *optic ataxia*. Indeed, the original formulation of the Action-Perception Model was in large parts built upon a single case of visual agnosia, the patient D.F., and the (putative) double dissociation of visual agnosia and optic ataxia.

Visual agnosia

The patient D.F. was suffering from carbon monoxide intoxication yielding damage in the occipitotemporal areas. Even though her IQ, speech abilities, and color perception were (largely) unaffected, she exhibited a marked loss of abilities in object recognition, extending to faces and even everyday objects. In particular, shape recognition was impaired, regardless of whether the shape was defined by color, intensity, motion, continuity, and so on; thus a case of visual (object) agnosia (Goodale & Milner, 2004b; Milner & Goodale, 1995, 2006; Milner et al., 1991). In a series of experiments, D.F. was unable to verbally judge the orientation of a small slot or match a comparison object to the desired orientation. In contrast, she had no problems placing her hands or the comparison objects into the very same slots (Milner et al., 1991). In another study, D.F. was unable to discriminate among objects, but showed no difficulty in placing her fingers to accurate positions when asked to grasp these objects (Carey, Harvey & Milner, 1996; Goodale et al., 1994). The grasp lines shown in Figure 2.1a were indeed very similar to those of a healthy control participant. Especially interesting is the fact that D.F. cannot use different dimensions or properties of objects to distinguish between them. Yet, her grip scaled adequately to the same dimensions if asked to grasp the objects (Goodale, Milner, Jakobson & Carey, 1991). Goodale et al. (1991) interpreted this dissociation in a way that D.F.'s lesion impaired her perceptual abilities mediated by occipitotemporal areas (thus the ventral stream), but left unaffected her visuomotor abilities processed in the dorsal stream. One can even say that the Action-Perception Model initially was inspired by these findings. Goodale et al. (1994) have further reported detoriated grasping performance (e.g., loss of pre-shaping) in D.F. in the case of delayed grasping. Although counterintuitive at first glance, this does make sense in the light of the real-time view of the dorsal stream (see Sections 2.1 and 2.4): the unavailability of immediate visual input requires the reliance on previously established percepts. And these are provided by the ventral stream, which is lesioned in D.F. Note that subsequently other visual agnostic patients, with even better preserved visuo-motor abilities have been described (e.g., Dijkerman, Lê, Démonet & Milner, 2004).



(a) (b)

Figure 2.1: The grasp lines (i.e., lines connecting the initial contact points of the thumb and the index-finger) of (a) the visual agnostic patient D.F., and (b) the optic ataxic patient R.V. (figure adopted from Goodale et al., 1994).

Still, it is not entirely clear how to best characterize the performance pattern of D.F. Schenk (2006) pointed out that the typical tasks for testing perception or action required either allocentric or egocentric spatial metrics. Disentangling this confound, he found impaired performance in D.F. when the tasks required allocentric rather than egocentric spatial metrics – regardless of whether the task was a perceptual or action one. This pattern of results suggests an allocentric deficit (plus preserved egocentric abilities) in D.F., thus weakening a crucial, yet not the sole, piece of evidence for the Action-Perception Model.

Optic ataxia

The opposite pattern of loss of abilities is shown by patients with optic ataxia, originally described as a part of the Bálint syndrome (Bálint, 1909). Optic ataxia follows damage to the PPC, or more precisely the parieto-occipital-junction (Jeannerod, 1986; Perenin & Vighetto, 1988; Pisella et al., 2009), and is characterized by marked deficits in visually guided (but not auditorily guided) movements directed to the visual periphery of the contralateral visual field. In addition to this 'field effect', damage to the left hemisphere results in right-hand problems for movements into both visual fields ('hand effect'). Specific problems arising during grasping movements are inappropriate grasping points plus an extremely large grip aperture, without any correlation with the actual target size (Jeannerod, 1986). These problems are more pronounced when the target objects are neutral or unfamiliar (Jeannerod, Decety & Michel, 1994). Importantly, these problems are not due to pure sensory or motor problems, and have thus been described as a specific sensorimotor deficit (e.g., Rossetti, Pisella & Vighetto, 2003). In contrast, the same patients do not have problems recognizing or discriminating between objects. In the abovementioned study by Goodale et al. (1994) the optic ataxic patient R.V. was tested, too. In striking contrast to D.F.'s performance, she had no problems dicriminating the curvy objects. At the same time, when asked to grasp these objects, she was not able to select appropriate grasp points (see Figure 2.1b). Moreover, and in contrast to the visual agnostic patient D.F., optic ataxic patients show improved grasping (or reaching) accuracy after a delay (Milner, Paulignan, Dijkerman, Michel & Jeannerod, 1999), especially for targets presented in the visual periphery (Rossetti et al., 2005). Interestingly, the longer the delay the more improves the accuracy (Himmelbach & Karnath, 2005), suggesting a more gradual than an abrupt change from a dorsal to a ventral mode of action planning in the absence of direct visual input (Goodale, Westwood & Milner, 2004; Hu & Goodale, 2000) (see Section 2.4).

The observable deficit in optic ataxia has first been ascribed to impaired programming (Jakobson, Archibald, Carey & Goodale, 1991). Yet, recent studies cast doubt on this interpretation and suggest an interesting alternative. Pisella et al. (2000) were probably the first to demonstrate a deficit in central vision in optic ataxia, namely the inability to respond fast and automatically to target dislocations – a behavior that is usually observed in healthy people, even under conflicting instructions. In contrast, deliberate, but costly, late corrections were not disrupted. Hence it was suggested that it is not the programming but rather the online correction mechanism that fails in optic ataxia (Pisella et al., 2000; Rossetti et al., 2003). Since peripheral vision is less accurate than central vision, this would explain the dominance of peripheral problems in optic ataxia. Khan et al. (2005) further point out that what matters is not the original presentation location (central or peripheral), but rather the location after gaze-based location transformations. In sum, if such results replicate and the interpretation advanced by Pisella et al. (2000) and Rossetti et al. (2003) is a valid one, this clearly undermines the role of the *PPC* in the real-time planning of actions as suggested by the Action-Perception Model (Milner & Goodale, 1995, 2006).

Visual agnosia and optic ataxia: a double dissociation?

The cases of visual (object) agnosia and optic ataxia (see also Newcombe et al., 1987) have since been interpreted as a double dissociation and as providing compelling evidence for the Action-Perception Model. Still, doubts have been raised recently concerning the exact interpretation of the putative double dissociation. Most scepticism comes from the fact that the visuomotor abilities of optic ataxic patients have almost only been tested for peripheral vision, but the perceptual abilities of visual agnostic patients only for central vision. In addition, mere peripheral perception appears indeed to suffer from *PPC* lesions (Pisella et al., 2009). These results and ideas undermine the conclusion of a clear-cut interpretation in terms of action *vs.* perception, but rather allow for an interpretation in terms of peripheral *vs.* central vision (Pisella, Binkofski, Lasek, Toni & Rossetti, 2006; Pisella et al., 2009; Rossetti et al., 2003).

2.2.2 Imaging studies

The recent development in neuroimaging techniques (such as fMRI) has significantly advanced our knowledge on the functional organization of the brain. Since the present work does not make use of imaging techniques, I will only give a rather brief discussion of some relevant results. The interested reader I like to refer to Milner and Goodale (2006). In general, analyses of human extrastriate areas have revealed a good correspondance of the human and the macaque visual systems, and in particular have supported the distinction into a ventral and a dorsal stream within the human cortex (Tootell et al., 2003).

The original assumption of a lesioned ventral stream in the patient D.F. (Goodale et al., 1991) was of course hypothetical, since not much was known about the exact cortical structures beyond $V1$ in the human cortex and imaging techniques were not far developed. Some early imaging studies nevertheless supported this contention, but their spatial resolution was insufficient to exactly localize the lesion. James, Culham, Humphrey, Milner and Goodale (2003) have re-examined D.F. using high-resolution fMRI and confirmed a bilateral lesion of *lateral occipital areas (LO).* In further accordance with the Action-Perception Model, several object-selective areas have been identified within the ventral stream (see Grill-Spector, 2003), among them the FFA (Kanwisher et al., 1997) and the PPA (Epstein & Kanwisher, 1998). Irrespective of whether such areas are specialized modules for specific object categories such as faces, or are better characterized as emergent areas of expertise (Tarr & Gauthier, 2000), it is clear that these findings support the notion of the ventral stream as being necessary for object recognition. More direct support comes from a recent study showing that parts of area *LO* treat varying views of objects as equivalent (James, Humphrey, Gati, Menon & Goodale, 2002), a feature clearly necessary for successful object recognition. Similarly, McKyton and Zohary (2007) reported that object location is coded in area *LO*, too, with constant coding during eye movements. This result is in accordance with the assumption that the spatial location of objects is not exclusively coded in the dorsal stream, but also in the ventral stream (Goodale & Milner, 1992; Milner & Goodale, 1995, 2006).

The *PPC* is well located to receive visual and somatosensory input and to project into pre-motor and motor areas (Culham, Cavina-Pratesi & Singhal, 2006) and thus has been described as a somatosensory interface for planning and controlling visually guided movements (e.g., Buneo & Andersen, 2006). Similar to the ventral stream's object-specific areas, in monkeys areas within or near the *intraparietal sulcus (IPS)*[2] have been implicated in specific motor actions, such as saccades (*lateral intraparietal area (LIP)*), reaching (*parietal reach region (PRR)*), or grasping (*anterior intraparietal area (AIP)*) (Connolly, Andersen & Goodale, 2003; Culham & Kanwisher, 2001). Subsequent work has further identified

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[2] The *IPS* divides the *PPC* into its inferior and superior part.

human homologues and related the human *AIP* specifically to grasping (but not, e.g., to reaching) movements (Castiello, 2005; Culham et al., 2006, 2003). In particular, preshaping during grasping activated *AIP* more than reaching did, but for the ventral area *LO* no difference between grasping and reaching was reported by Culham et al. (2003). These authors interprete this pattern as evidence that the *AIP* performs the computations necessary for a (pre-shaped) grasping movement, without additional help from the ventral stream, in particular area *LO*. Other research suggests a role of the *PPC* in online corrections of ongoing movements, by demonstrating disruptions of normally observed corrections following application of *transcranial magnetic stimulation* to the *PPC* (Desmurget et al., 1999). Such findings are, however, also well in line with the interpretation of optic ataxia put forward by Pisella et al. (2000) and Rossetti et al. (2003).

2.2.3 Summary of neuropsychological evidence

In the previous sections I have reviewed several lines of evidence for the Action-Perception Model from neuropsychological disorders plus recent findings from neuroimaging studies. The neuropsychological evidence has not remained uncontroversial to date (e.g., Pisella et al., 2006, 2000; Schenk, 2006), and the exact interpretation of the (putative) double dissociation of visual agnosia and optic ataxia requires further careful investigations. On the other hand, imaging results are mostly in accordance with what can be expected based on the Action-Perception Model.

Whatever the eventual outcome of the thus far discussed evidence will be, the proposed distinction of action and perception should also leave traces in healthy people. Based on the ego- *vs.* allocentric frames of reference, in which the dorsal and the ventral stream, respectively, shall code spatial locations, a different effect of visual illusions on action and perception has been proposed. This will be the topic of the next section.

2.3 A dissociation of action and perception in healthy people: the effect of visual illusions

According to the Action-Perception Model, the ventral perception stream codes spatial locations in allocentric coordinates (see Section 2.1; or Goodale and Milner (2004b), Milner and Goodale (1995, 2006)). Thus, in perceptual tasks, size-contrast illusions deceive the perceptual system and yield a non-veridicial size estimation. A famous example is the

Ebbinghaus illusion (see Figure 2.2), sometimes also called the Titchener illusion (but see Burton, 2001): even though the inner circles are physically of identical size, the one surrounded by smaller circles is perceived as larger than the one surrounded by larger circles (e.g., Levine, 2000; Roberts, Harris & Yates, 2005). What when acting upon an object? Clearly, it would be disadvantageous if our actions are fooled by size-contrast illusions. It has been argued though that exactly this does not happen, since the dorsal action stream takes only relevant egocentrically coded coordinates into account, and disregards much (if not all) of the environment in which the targets are embedded.

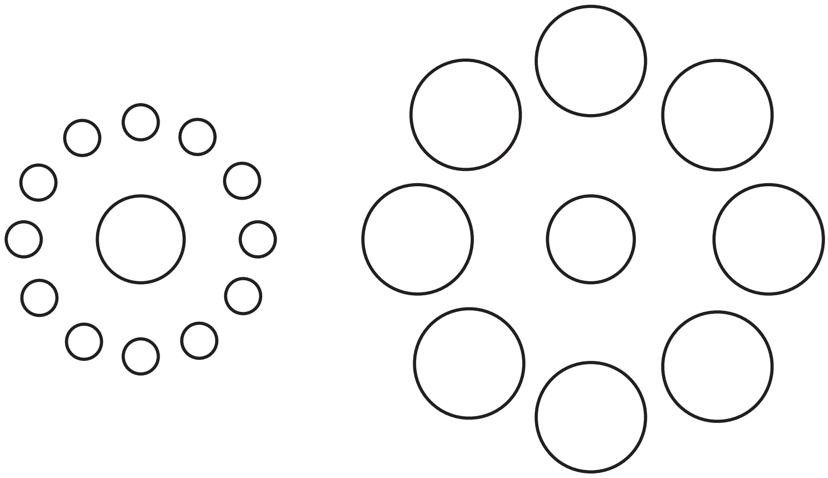

Figure 2.2: The Ebbinghaus illusion as an example for size-contrast illusions: both inner circles are physically of identical size. However, the one surrounded by smaller circles (left) is perceived as larger than the one surrounded by larger circles (right).

Aglioti et al. (1995) were the first to test this prediction[3]. They presented their participants with a modified version of the Ebbinghaus illusion in which the inner circle was a thin chip (instead of a drawn circle). In their perceptual task the participants exhibited an illusion effect of roughly 2.5mm. In contrast, when the participants grasped the chip the illusion effect on the MGA was only 1.5mm, thus smaller than the perceptual effect, and the authors concluded that this pattern supports the Action-Perception Model. This result was later replicated under open-loop conditions and with a different perceptual task (manual estimation: participants are asked to indicate the size of the target with their thumb and index-finger) by Haffenden and Goodale (1998) and Haffenden, Schiff and Goodale

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[3] This is not the whole truth to the story, since earlier studies by Bridgeman, Lewis, Heit and Nagle (1979) and Mack, Heuer, Villardi and Chambers (1985) are already informative to this idea. However, it is fair to say that the study by Aglioti et al. (1995) was the first explicitly motivated by the Action-Perception Model – and is also the one taking most of the credit.

(2001). Comparable results were also reported – among others – from grasping (for a review, see Bruno & Franz, 2009) or pointing at (for a review, see Bruno, Bernardis & Gentilucci, 2008) the Müller-Lyer illusion, or grasping a bar embedded in the Judd illusion or presented against the background of a Ponzo illusion (Ellis, Flanagan & Lederman, 1999; Ganel, Tanzer & Goodale, 2008). Notably, there are studies where the illusion effect on the perceptual measure was much larger than on the MGA (e.g., Haffenden et al., 2001; Haffenden & Goodale, 1998).

On the contrary, others were not successful in replicating larger illusory effects on perception than on action (e.g., Franz, 2003a; Franz, Bülthoff & Fahle, 2003; Franz, Fahle, Bülthoff & Gegenfurtner, 2001; Franz, Gegenfurtner, Bülthoff & Fahle, 2000; Pavani, Boscagli, Benvenuti, Rabuffetti & Farnè, 1999), and the claims of support for the Action-Perception Model have been criticized on various grounds. In the remainder of this section I will discuss the most important criticisms (for more details and reviews of this controvery, see Carey (2001), Franz (2001), Franz and Gegenfurtner (2008), Goodale (2008), Goodale, Gonzalez and Króliczak (2008), or Smeets and Brenner (2006)):

- In the study by Aglioti et al. (1995) the perceptual measure involved a comparison of two illusion setups, but the action task involved only one such setup. It was argued that the kind of task was thus confounded with attentional demands, and in fact, equating the attentional demands, diminished the difference in the illusion effects for action and perception (Franz, 2003a; Franz et al., 2001, 2000; Pavani et al., 1999).

- Most of the studies unequivocally report a small illusory effect on the MGA (see Bruno & Franz, 2009; Franz & Gegenfurtner, 2008), sometimes even significant from zero. The Action-Perception Model, however, does not – in a strict sense – predict *any* illusory effect on action. To reconcile, Haffenden et al. (2001) argued that this happens when the surrounding circles are treated as obstacles. Testing this assertion, Franz et al. (2003) concluded that obstacle-avoidance is not the reason for the illusory effect on grasping.

- I have already mentioned that several studies report much larger illusory effects on perception than on the MGA (e.g., Haffenden et al., 2001; Haffenden & Goodale, 1998). In fact, it is tempting to say that all these studies use the manual estimation procedure as the perceptual measure. As it turned out, manual estimation responds to a physical or illusory change of size of the target objects much more than other, classical (psychophysical), procedures (Franz, 2003a). The larger slope of the response function can then explain the larger illusory effect on perception compared to action. Franz (2003a) and Franz and Gegenfurtner (2008) argued that the illusion effect needs to be corrected by division through the slope of the response function. Such corrected illusion effects indeed are of the same size as those reported for the action tasks.

- Other authors suggested that the smaller (or absent) illusion effect on action is simply due to the possibility of online-control mechanisms fine-tuning the movement in-flight (Post & Welch, 1996). In their meta-analysis of 18 studies on the Müller-Lyer illusion, Bruno and Franz (2009) also concluded that this provides the most parsimonious explanation for the whole pattern of results.

- Yet others argued that for grasping the system does not take into account the size of the target objects, but only computes the grasp points. As a consequence, the MGA would not be an ideal dependent measure (Brenner & Smeets, 1996; Jackson & Shaw, 2000; Smeets & Brenner, 1999, 2006; Smeets, Brenner, de Grave & Cuijpers, 2002). As size predicts weight, these authors used grip or lift force as the dependent measure and revealed an illusory effect on grasping in the expected direction: objects perceived as larger were grasped and lifted with more force, than those perceived as smaller (Brenner & Smeets, 1996; Jackson & Shaw, 2000).

- Lastly, as I reviewed in Section 2.2.1, several authors suggested that the performance increase with (delayed) movements in optic ataxic patients is due to a reliance on the (spared) perceptual mechanisms provided by the ventral stream (Milner et al., 1999; Rossetti et al., 2005). This implies that these patients should show sensitivity to visual illusions in their actions. However, this was not the case in a study by Coello, Danckert, Blangero and Rossetti (2007), although it is left unclear whether one can expect the switch to a ventral mode in non-delayed action tasks.

Against the background of these criticisms it appears that the current state of research is insufficient to give a definite answer on whether or not the proposed dissociation of visual illusions on action and perception exists. Still, far-reaching conclusions have been based on the absence or presence of illusion effects in action tasks. In the next section some examples will be given, for further examples I refer the reader to Chapters 4 and 6.

2.4 Does the dorsal stream operate only in real-time?

As explained in Section 2.1 the dorsal stream is thought to be involved in the fast visuomotor transformations for planning and controlling movements under full vision. This translates to viewing the dorsal stream as a system that only operates in real-time and without memory reliance, thus it can only use the information available at the time a movement is to be executed. In turn, this assumption has two interesting consequences.

First, what happens if one needs to grasp a memorized object? Needless to say, this is not a big trouble: we can pretend to grasp an object, and even grasp it after our vision of this object has been removed. In this case, however, the dorsal stream – requiring direct visual input – cannot be recruited. Goodale, Jakobson and Keillor (1994) had their participants to pretend grasping an object after a short delay of two or more seconds (the object was removed during the delay, preventing haptic feedback for the participants), or to pantomime grasping. Kinematics of these grasping movements differed from those in normal grasping and the authors tentatively suggested that the movements were grounded on memorized perceptual information instead. Similar findings of qualitative differences between normal and delayed grasping were later reported by Hu, Eagleson and Goodale (1999), reinforcing the previous tentative claim of Goodale et al. (1994). In a follow-up study, Hu and Goodale (2000) used a simple size-contrast illusion (the target object was flanked by another, smaller or larger, object) and found that the MGA of delayed grasping (but not of visually guided grasping) was affected by the deceiving flanker object. They concluded that grasping after a delay relies on allocentric coordinates, and suggested an abrupt shift from a dorsal to a ventral mode of processing, once direct vision is not available when the movement should be initiated (see also Goodale et al., 2004). The same conclusion was reached by Westwood, Heath and Roy (2000) and Westwood and Goodale (2003). These authors showed that action is unaffected by the Müller-Lyer illusion as long as vision is available at the moment of response initiation. In contrast, they found an illusory effect once vision was not available at that point of time. In addition, the illusory effect was then comparable with or without an additional preceding delay. Thus, if no vision of the target object is available at the moment of a movement's initiation, the ventral stream needs to pitch in and to provide the required information.

Other researchers suggested that the differences in kinematics of normal and delayed grasping (e.g., larger MGA) are due to a simple decay of information, rather than a (qualitative) shift from a dorsal to a ventral mode of action planning. Carefully controlling the amount of visual feedback, experimental work seems to support this interpretation (Hesse

& Franz, 2009). In particular, the MGA can nicely be fitted to an exponential function of the amount of delay – a pattern well known for memory decay. The illusion effect on MGA (at least for the Müller-Lyer illusion) has also been shown to be a function of available visual feedback during the grasping movement (Franz, Hesse & Kollath, 2009). These studies suggest at least a more gradual rather than the proposed abrupt shift, if not even a single, but decaying, representation used in visually guided and in delayed grasping (see also Himmelbach & Karnath, 2005).

A second consequence of the real-time view is that, unlike other visual processes, visually guided movements should not be influenced by previously seen objects. Craighero, Fadiga, Umiltà and Rizzolatti (1996) and Craighero, Fadiga, Rizzolatti and Umiltà (1998) reported experiments in which grasping (an invisible) object was faster if a prime with a congruent orientation was presented briefly before the go-signal. At first glance this clearly contradicts the real-time view favored by Milner and Goodale (1995, 2006). But, as discussed above, grasping an invisible object relies on a memorized representation, thus escapes the real-time operations of the dorsal stream. Cant, Westwood, Valyear and Goodale (2005) used visible objects and found no evidence for a priming effect in visually guided grasping, but only in memory-based (delayed) grasping. Moreover, the same primes had a strong priming effect in a classic naming task. Taken together, Cant et al. (2005) reached at a conclusion well in line with the predictions derived from the real-time view (see also Goodale, Króliczak & Westwood, 2005). As Hesse, de Grave, Franz, Brenner and Smeets (2008) pointed out, all these results were based on response time analyses, and may thus not convey the full story. In their experiment, the kinematics of grasping movements were recorded, too, and exhibited an influence of previously seen prime objects, indeed even in response times (see also Whitwell & Goodale, 2009, for a similar finding). In sum, it appears unclear whether visually guided movements are or are not influenced by previously encountered objects.

To summarize, the evidence for the real-time assumption of the dorsal stream is mixed at best, and I consider it premature to give a definite answer to this issue. However, it is clear that from early on the possibility was included in the Action-Perception Model that not all actions are based on the dorsal stream. In particular, pantomimed and delayed grasping movements were suggested to rely on the perceptual information provided by the ventral stream (Goodale et al., 1994, 2004; Hu & Goodale, 2000).

2.5 Is dorsal processing automatic?

Processing in the ventral stream is assumed to be far more resource-demanding and conscious than processing in the dorsal stream, which is generally assumed to work fast, automatic, and unaffected by any capacity limitations (e.g., Enns & Liu, 2009; Goodale & Milner, 2004b; Jeannerod & Jacob, 2005; Liu, Chua & Enns, 2008; Norman, 2002). Given that typical dorsal tasks, such as grasping an object, are highly practiced and skilled, this appears intuitive at first glance. However, as intuitive this claim might be, empirical studies are rather rare and their results do not provide an unambiguous picture.

For example, Singhal, Culham, Chinellato and Goodale (2007) combined in two experiments visually guided grasping and delayed (thus memory based) grasping with two different secondary tasks. Although the degree of interference with the secondary task was larger for delayed grasping, there was also considerable dual-task interference for visually guided grasping. This should not be the case if dorsal processing does not require (central) processing resources. On the other hand, Liu et al. (2008) combined a (dorsal) pointing task with a rapid serial visual presentation (RSVP) task and concluded from their results that dorsal processing does not share resources with ventral processing. Recently, these results have been replicated for young adults, not though for old adults (Lee & Hsieh, 2009). Another widely used methodological tool to investigate dual-task interference is the PRP paradigm. Although I will introduce this paradigm only in the next chapter in more detail, let me briefly discuss the study by Kunde, Landgraf, Paelecke and Kiesel (2007) already here. These authors used a perceptual judgment and a grasping task (Ganel & Goodale, 2003; see also Section 2.6) within a PRP experiment, with (as is most common) a binary tone classification as the concurrent other task. It turned out that both tasks showed about the same degree of interference from the tone classification task. Hence, according to this study, dorsal processing, though seemingly fast and effortless, is subject to capacity limitations and therefore cannot be construed as automatic. Unfortunately, the results of this study are open to at least two alternative accounts, and one goal of the present research is to further pursue the PRP approach and to thorougly test these alternatives (see Chapters 4 and 5 for more details).

2.6 Identifying ventral processing: Garner-Interference

The absence or presence of illusory effects on action has been used to indicate a dorsal *vs.* ventral processing mode, respectively (e.g., Gonzalez, Ganel & Goodale, 2006; Gonzalez, Ganel, Whitwell, Morrissey & Goodale, 2008; Hu & Goodale, 2000). However, in the light of the controversy still surrounding this effect, application of different indicators is desirable to enable firmer conclusions. In Section 2.1 I have mentioned the distinction into analytical and holistic processing (Ganel & Goodale, 2003), from which, I will argue, a possible alternative indicator for ventral processing can be derived – which can be characterized as a variant of *Garner-Interference*.

Ganel and Goodale (2003) argued that visual perception would not be successful if given dimensions of an object are perceived isolated from other dimensions of the same object (= "holistic processing"). In contrast, object-directed actions should only take action-relevant dimensions into account and not be misled by irrelevant dimensions (= "analytical processing"). In other words, the ventral stream is seen to process input in a holistic manner, whereas the dorsal stream processes the input analytically and is more efficient at ignoring variations of task-irrelevant stimulus dimensions.

This idea has nicely been demonstrated by Ganel and Goodale (2003) using a variant of Garner's speeded classification task (Garner, 1974, 1978), or more precisely, a filtering task (Posner, 1964). In such a Garner task, participants are to classify stimuli according to one relevant dimension, while ignoring another task-irrelevant dimension. Critically, this is done under two experimental conditions: (1) in the *baseline* condition, the irrelevant dimension remains constant, whereas (2) in the *filtering* condition this irrelevant dimension varies. If the irrelevant dimension can effectively be ignored (i.e., this dimension is filtered and the stimulus can be perceived analytically), baseline and filtering conditions should produce the same response times. In contrast, if the irrelevant dimension cannot be ignored (i.e., the stimulus is perceived holistically) response times are longer in the filtering than in the baseline condition (= "Garner-Interference").

Ganel and Goodale (2003) applied this logic to two tasks that were assumed to rely on either ventral or dorsal processing. In the ventral *perceptual judgment* task the participants were to judge the width of rectangular wooden blocks, and in the dorsal *grasping* task the same wooden blocks were grasped across their width. Four target objects were constructed according to a factorial combination of two lengths (63 and 75mm) and widths (30 and 35.7mm; see also Felfoldy, 1974). A schematic illustration is given in Figure 2.3. Note that the objects' width was always the relevant dimension, and the objects' length was the irrelevant dimension. During baseline conditions only blocks of the same length were used as stimuli (i.e., either a/b or c/d of Figure 2.3); during filtering conditions all four blocks were used.

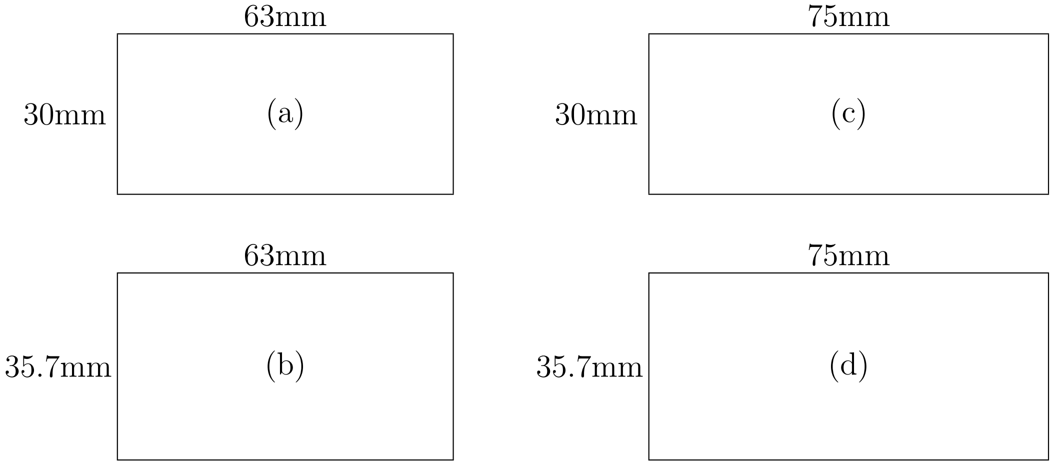

Figure 2.3: Schematic illustration (not drawn to scale) of the wooden blocks used in the study by Ganel and Goodale (2003). In the baseline condition only blocks of same length (the irrelevant dimension) were used (i.e., either a/b or c/d) while in the filtering condition all four blocks were used (see text for more details).

Garner-Interference (i.e., longer response times in filtering than in baseline conditions) was only observed for the perceptual judgment task, but not for the grasping task[4]. In other words: varying a task-irrelevant stimulus dimension affects response times in a ventral, but not in a dorsal task, which appears able to efficiently ignore these variations. In a second experiment Ganel and Goodale (2003) found Garner-Interference for simulated grasping movements, that have earlier been ascribed to the ventral stream (Goodale et al., 1994). Subsequently, Kunde et al. (2007) have used the grasping and the perceptual judgment task in a dual-task study. Even though the main purpose of this study was different (see Section 2.5), it is noteworthy that even under dual-task conditions Garner-Interference was found for the ventral, not though for the dorsal task.

It thus seems that the presence (or absence) of Garner-Interference may be better suited for indicating an underlying ventral or dorsal processing mode than the controversial effect of visual illusions is. The present experiments will use Garner-Interference to distinguish between both processing modes (see Chapter 4 for more information).

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[4] Ganel and Goodale (2003) also reported no differences between the baseline and the filtering conditions in kinematic measures such as the MGA. However, I will focus in the present experiments on response times, since only these are directly comparable across grasping and perceptual judgment tasks.

2.7 Chapter summary

The Action-Perception Model (Goodale & Milner, 1992) ascribes to the dorsal stream the role of vision for action, and to the ventral stream the role of vision for perception. I have first reviewed the neuropsychological evidence on which the Action-Perception Model was initially mainly based. I then turned to evidence from studies with healthy people, in particular to the effects of a delay between sight of an object and grasping it, and the effects of visual illusions on action and perception. It is fair to conclude that the evidence is still mixed. The last two sections are especially important to the present work. In Section 2.5 I discussed the few available studies on whether dorsal processing is automatic – as has been claimed – or not. In Section 2.6 I introduced Garner-Interference as a potential (behavioral) indicator for an underlying dorsal or ventral processing mode. Compared to the putative diverging effect of visual illusions on perception and action, Garner-Interference is thus far undisputed and will here be used as an empirical index for a ventral stream contribution to action. I will now continue with introducing a methodological tool to assess dual-task interference: the PRP paradigm. This particular paradigm underlies most of the experiments I will present in Chapters 5 and 6.

3 Analyzing dual-task performance: the 'psychological refractory period' (PRP)

A central purpose of the present work touches the dual-task characteristics of vision for action, i.e., the susceptibility of dorsal processing to interference from concurrent tasks. Research with continuous tasks has suggested possible dual-task performance without performance deterioration in one or both tasks (e.g., Spelke, Hirst & Neisser, 1976). It remains unclear though, as to whether such findings imply real parallel processing of two tasks, or simply a plan-and-buffer strategy with (rapid) task-switching (Pashler & Johnston, 1989, 1998). More telling about (limitations of) dual-task performance are tasks in which (1) a response can unambigiously be related to one stimulus and (2) the degree of the tasks' overlap can be manipulated.

Such a task was first used by Telford (1931) whose subjects responded manually to an auditory stimulus (his Experiment 1). The time between two successive stimuli ('stimulus onset asynchrony', SOA) was either 0.5, 1, 2, or 4 seconds. Response times were longer at an SOA of 0.5 seconds (thus with considerable task overlap in relation to the preceding stimulus) than at the longer SOAs. Similar results were obtained regarding the accuracy of magnitude judgments in Telford's Experiment 2. In analogy to upcoming physiological evidence, Telford (1931) suggested a *psychological refractory period (PRP)* as the primary reason for these results: a temporary inability to process a task shortly after finishing a preceding task. The slowing down of responses at short SOAs was later labeled the *PRP effect*. Yet, he correctly recognized that the "refractory and hyper-excitable periods are but names given to the phenomena which must themselves be explained" (Telford, 1931, p. 33). A step towards this goal was subsequently made by Welford (1952) and later by Pashler (1984, 1994).

In Section 3.1 I will first describe the presently used variation of Telford's (1931) task, now known as the PRP paradigm. This often-used paradigm provides researchers with means to investigate dual-task performance and its temporal micro-structure. Several models and theoretical accounts have been put forward to explain the robust effects observed with this paradigm, and I will discuss them in Section 3.2. An additional advantage of the PRP paradigm is that it can also be used to localize the emergence of experimental effects within the processing stream of a task. The two procedures that are of some relevance to the present work will be introduced in Section 3.3.

3.1 The PRP paradigm and the PRP effect

3.1.1 The current research paradigm

Following the early work by Telford (1931) and Welford (1952), the study of the PRP effect has experienced a revival in the 1980ies. However, whereas Telford (1931) utilized a stream of 100 stimuli (and their related simple responses), the currently most prevalent experimental setup differs in some aspects. Typically, on every trial two different tasks T_1 and T_2 are performed, both with their own imperative stimuli (S_1 and S_2, respectively) and responses (R_1 and R_2, respectively). Both stimuli are presented in rapid succession, with the elapsed time from S_1 to S_2 onset refered to as the SOA. Typically, the SOA varies from 0 ms to 1000 ms, and is manipulated either blockwise or randomly interleaved within blocks. Response times (RT_1 and RT_2, respectively) are measured from stimulus onset until the related response is given. The time between R_1 and R_2 is denoted as the *interresponse interval (IRI)*. Instructions most often stress speed and accuracy, and give priority to T_1 processing. The time course of a typical PRP experiment is illustrated in Figure 3.1.

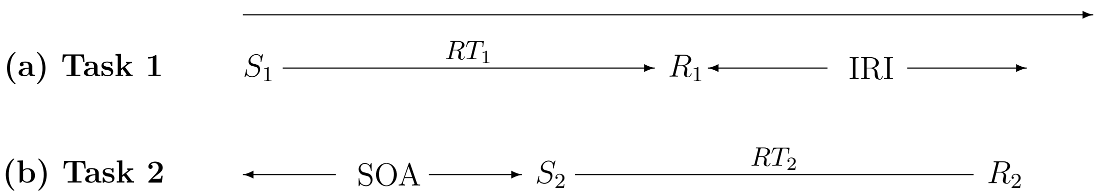


Figure 3.1: Time course of events in a typical PRP experiment. (*Note:* S_1, S_2, R_1, R_2, RT_1, and RT_2 denote stimuli, responses, and response times of Tasks 1 and 2, respectively; SOA = stimulus onset asynchrony; IRI = interresponse interval)

3.1.2 Empirical observations with this paradigm: the PRP effect

The paradigm I just described in Section 3.1.1 has been employed in a tremendous number of studies. Despite the number of different tasks, stimuli, and responses, two typical findings are commonly reported (see Figure 3.2 for an illustration): whereas RT_1 remains largely unaffected by the SOA manipulation, RT_2 shows a large increase at shorter SOAs (the PRP effect). The increase in RT_2 has sometimes a slope of -1 at sufficiently short SOAs. At times, the PRP effect is quantified as the difference in RT_2 with short and long SOAs, i.e.,

$$PRP := RT_{2|\text{shortest SOA}} - RT_{2|\text{longest SOA}} \tag{3.1}$$

The PRP effect is usually seen to arise because both tasks require a common capacity-limited resource or a processing stage that can be accessed by only one of the two tasks at any time (see Section 3.2 for more details). Absence of the PRP effect is sometimes interpreted in a way that at least one of the two tasks makes no use of this stage or resource. This is, however, not necessarily true, and is a valid claim only under special circumstances, such as long RT_1 (Lien, McCann, Ruthruff & Proctor, 2005b).

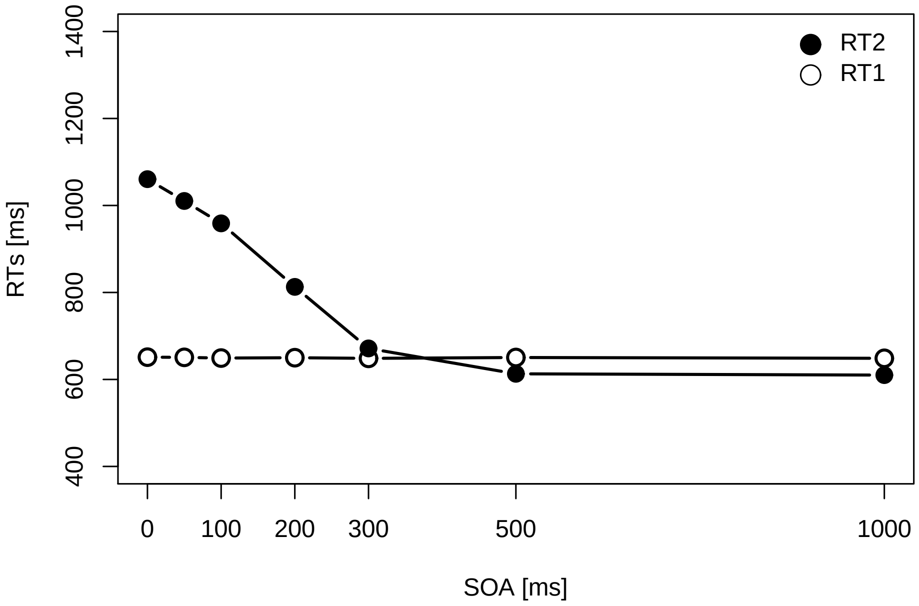


Figure 3.2: Idealized illustration of response times (RT) typically reported from PRP experiments. The PRP effect refers to the increase of RT_2 with a decreasing SOA (stimulus onset asynchrony).

The PRP effect itself is a remarkably robust phenomenon and has been reported from a number of tasks, among others, mental rotation (Heil, Wahl & Herbst, 1999; Ruthruff, Miller & Lachmann, 1995; van Selst & Jolicoeur, 1994), word production (Ferreira & Pashler, 2002), word selection (Ayora, Janssen, Dell'Acqua & Alario, 2009), word recognition (Lien et al., 2006), the stopping of actions (Horstmann, 2003), emotion processing (Tomasik, Ruthruff, Allen & Lien, 2009), hedonical choices (Pashler, Harris & Nuechterlein, 2008), or highly trained actions like braking a car (Levy, Pashler & Boer, 2006). It resists intense practice (Ruthruff, Johnston & van Selst, 2001; van Selst, Ruthruff & Johnston, 1999), perhaps in younger as well as older adults to the same extent (Allen, Ruthruff, Elicker & Lien, 2009; Maquestiaux, Hartley & Bertsch, 2004).

Apart from these, few studies reported exceptions from the PRP effect (for an overview, see Lien, Ruthruff & Johnston, 2006). Greenwald (1972) argued that capacity limited processes, such as response selection, do not play a role in ideomotor-compatible tasks. Ideomotor-compatible tasks are tasks wherein the stimulus closely corresponds to the response-contingent action effect, e.g., when one vocally produces an auditorily presented letter. Indeed, Greenwald and Shulman (1973) and Greenwald (2003) reported absence of a PRP effect when two such ideomotor-compatible tasks were combined. These findings, however, are difficult to interprete since their replication turned out being difficult (Greenwald, 2004, 2005; Lien, McCann, Ruthruff & Proctor, 2005a; Lien et al., 2005b; Lien, Proctor & Allen, 2002; Lien, Proctor & Ruthruff, 2003). A study by Pashler, Carrier and Hoffman (1993) with saccadic eye movements as R_2 is considered a second exception from the PRP effect. This study is of importance to the present experiments for two reasons. (1) Eye movements are a special response modality mediated by specific neural circuits, what strengthens the possibility that target-directed movements under dorsal control escape dual-task interference, too. (2) This study made use of a specific method, namely the introduction of negative SOAs, i.e., trials with a reversed task order. This methodological variation may be crucial to observe absence of PRP effects and will be used in one experiment here, too.

3.2 Theoretical accounts for the PRP effect

Since Telford (1931) suggested a refractory period to explain his results, several attempts were made to explain the PRP effect more precisely. The *central bottleneck model* was already envisaged by Welford (1952) and later further developed and formalized, most notably by Pashler and colleagues (Pashler, 1984, 1994; Pashler & Johnston, 1989, 1998). I will introduce this model in the next section, followed by shorter sketches of alternative models.

3.2.1 The central bottleneck model

Welford argued in his review that every task involves a central ”organizing time” (Welford, 1952, p.18), i.e., a stage of stimulus-response translation or response selection. To explain the PRP effect he suggested that ”no two central organizing times can overlap” (Welford, 1952, p.18), such that processing of T_2 needs to await until the central mechanisms are released from T_1. Additionally, central processes should be engaged from feedback produced by the responses (= 'response monitoring'). On the basis of a literature review, Smith (1967) came several years later to the same conclusion. Another 20 years later, Pashler and colleagues began to formalize a central bottleneck model from which many testable hypotheses were derived. In the current formulation (Pashler, 1994; Pashler & Johnston, 1989, 1998) the processing stream of each task is subdivided into three stages (see Figure 3.3): a pre-central stage A (e.g., perceptual processes), a central stage B (e.g., response selection or decisioning), and a post-central stage C (e.g., motor-related processes of response execution). Similar to the suggestion of Welford (1952), the crucial assumption

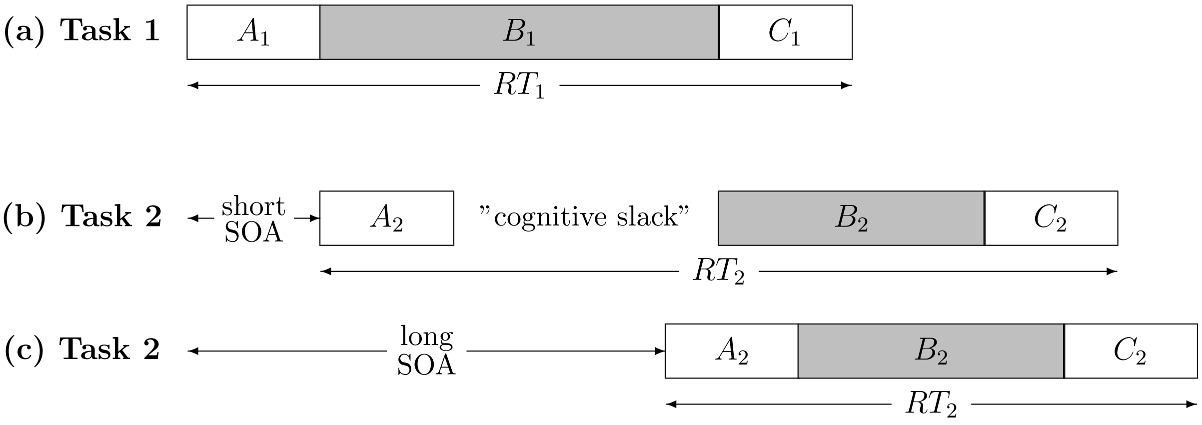


Figure 3.3: The central bottleneck model (e.g., Pashler, 1994): each task is subdivided into a pre-central stage A, a central stage B, and a post-central stage C. The PRP effect arises since with short SOAs Task 2 central processing needs to wait until Task 1 central processing has been finished (see text for more details; SOA = stimulus onset asynchrony).

is that no two central stages B can be processed at the same time, thereby constituting a central bottleneck. In contrast, pre- and post-central stages A and C can be processed in parallel to other processes. How does this model explain the typical results which I illustrated in Figure 3.2 (see also Pashler (1994) or, more formally, Schweickert (1978) or Schwarz and Ischebeck (2001))?

Let A_i, B_i, and C_i denote the durations of pre-central, central, and post-central stages of Task i. (For simplicity I assume a constant duration of all stages here. However, the predictions are essentially the same if stochastic variations are introduced.) According to Figure 3.3a, RT_1 is completely unaffected by the SOA manipulation, thus

$$RT_1 = A_1 + B_1 + C_1 \qquad \text{(see Figure 3.3a)} \tag{3.2}$$

Assuming that stage A_2 (the pre-central stage of T_2) begins as soon as S_2 is presented, two cases can be distinguished:

1. A_2 finishes *before* B_1 has been finished (i.e., $SOA + A_2 < A_1 + B_1$), a situation likely to occur with a short SOA (see Figure 3.3b). In this case stage B_2 needs to be deferred until after the central bottleneck has been released from stage B_1. The time from finishing A_2 until starting B_2 is called the *cognitive slack*, and this idle time is what yields the longer RT_2 at short SOAs.

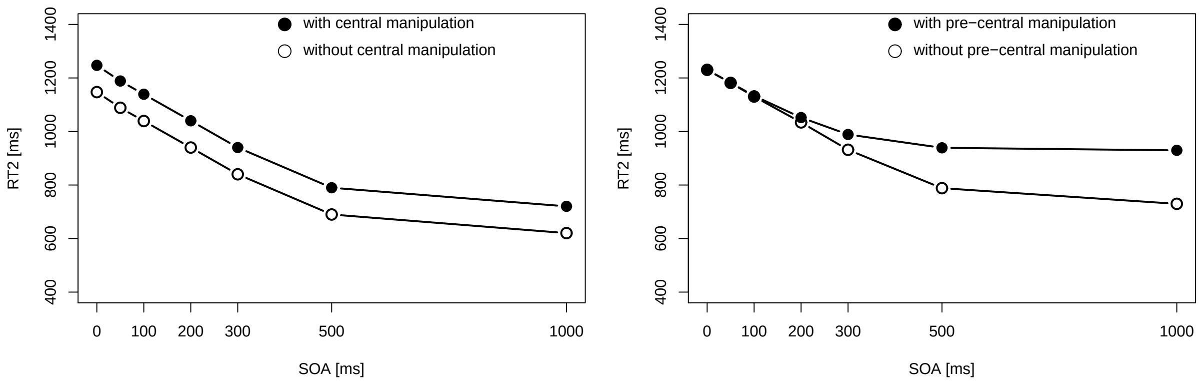
2. A_2 finishes only *after* B_1 has been finished (i.e., $SOA + A_2 \geq A_1 + B_1$), likely to occur at longer SOAs. In this case, no idle time of a cognitive slack occurs and stage B_2 can immediately begin after B_1 has been finished.

In sum

$$RT_2 = \begin{cases} A_1 + B_1 + B_2 + C_2 - SOA & \text{if } SOA + A_2 < A_1 + B_1 \qquad \text{(see Figure 3.3b)} \\ A_2 + B_2 + C_2 & \text{if } SOA + A_2 \geq A_1 + B_1 \qquad \text{(see Figure 3.3c)} \end{cases} \tag{3.3}$$

In fact, the RTs illustrated in Figure 3.2 are based on Equations 3.2 and 3.3 in a stochastic simulation. (For this simulation I assumed the length of central stages B_1 and B_2 as $\Gamma(k, \theta)$-distributed. All other lengths were deterministic.) This model makes several testable predictions that have been confirmed several times (for more details and reviews of empirical evidence, see, e.g., Koch, 2008; Pashler, 1984, 1994; Pashler & Johnston, 1989, 1998; Schwarz & Ischebeck, 2001; Schweickert, 1978). Some of these predictions have subsequently also been used to localize an experimental manipulation within the processing stream (see also Section 3.3; and Appendix A for a formal treatment of the following).

- Any manipulation that affects the duration of stage B_2 (= 'central manipulation') should have the same effect on RT_2 across all SOAs. In other words, a central manipulation and SOA should combine *additively*, as is illustrated in Figure 3.4a. Examples for such central manipulations are the complexity of stimulus-response translation or memory retrieval.
- If, in contrast, a manipulation affects the duration of stage A_2 (= 'pre-central manipulation') its effect on RT_2 varies with the SOA. If, with short SOAs, the cognitive slack is large enough, the now prolonged stage A_2 simply stretches into the slack time and has no effect on RT_2. This scenario is sometimes labeled *absorption into slack*. With longer SOAs, however, no such absorption can occur and RT_2 increases by the same amount as A_2 increased due to the manipulation. In sum, a pre-central manipulation and SOA should combine *underadditively*, as is illustrated in Figure 3.4b. Typical pre-central manipulations are stimulus contrast or brightness manipulations.



(a) (b)

Figure 3.4: Task 2 response times (RT_2) as predicted from the central bottleneck model (see Figure 3.3): (a) an additive interaction of SOA and a central manipulation, and (b) an underadditive interaction of SOA and a pre-central manipulation (SOA = stimulus onset asynchrony; see text for more details).

The original thinking of this processing bottleneck is that of a structural bottleneck, hardwired in human neuroanatomy and thus unavoidable. In contrast, more recent work claimed that the bottleneck is rather strategic. This means, that although parallel processing of two central stages could be possible, we deliberately defer T_2 central processes to, e.g., avoid crosstalk between tasks (Logan & Gordon, 2001; Meyer & Kieras, 1997). This implies that, in principle, it should be possible to obtain parallel processing under specific conditions. One study used excessive training and eliminated task overlap in stimuli and responses and claimed to provide evidence for a strategic bottleneck by showing virtually no interference between the tasks (Schumacher et al., 2001). Although convincing at first glance, methodological criticisms have been raised, and circumvening these, no parallel processing was observed (Levy & Pashler, 2001; Tombu & Jolicoeur, 2004). Recently, Ruthruff, Johnston and Remington (2009) used a 'deadline paradigm' and incentives to maximize efforts to process two tasks in parallel – if possible. Despite these efforts it was not possible to eliminate interference between tasks and the authors concluded that the bottleneck is a structural one (see also Ruthruff, Pashler & Klaassen, 2001).

3.2.2 Graded capacity sharing

At the other end of a continuum are resource models. Such models assume the existence of a limited central resource that can flexibly be allocated to different tasks. Thus two central stages can potentially be performed in parallel, yet not as efficient as in a single-task situation resulting in slowed (central) processing (McLeod, 1977; Navon & Miller, 2002; Tombu & Jolicoeur, 2003). According to such models, the PRP effect is due to dedicating resources initially to T_1 (central) processing, such that no (or at least less) capacity is available for T_2.

A formalized capacity sharing model has been put forward by Tombu and Jolicoeur (2003). In this model, the degree of capacity sharing during central stages is reflected in a model parameter varying from 0 to 1. Note that when all capacity is allocated to T_1 first, the central bottleneck model (see Figure 3.3) becomes simply a special case of the capacity sharing model. Theoretically interesting, both models only differ with regards to their RT_1 predictions: whereas the strictly serial central bottleneck model predicts no effect of SOA on RT_1 (see Equation 3.2), the capacity sharing model predicts increasing RT_1 with short SOAs (see Tombu & Jolicoeur, 2002, 2003, 2005). Although promising, only few attempts have been made to directly test this model. Positive evidence came mainly from the studies by Tombu and Jolicoeur (2002, 2005); in many other PRP studies the effects of SOA on RT_1 are not consistent, and sometimes even reversed. In addition, results from electrophysiological and neuroimaging studies are easier to reconcile with (central) bottleneck models than with resource models. Jentzsch, Leuthold and Ulrich (2007) and Osman and Moore (1993) used the lateralized readiness potential (Coles, 1989) and suggested from their results that a true bottleneck stage exists prior to the motor stage. There is also no increased activity in brain areas implicated in central executive control processes at short compared to long SOAs (Jiang, Saxe & Kanwisher, 2004). This was interpreted as evidence that T_2 simply is queued, instead of being processed (partly) in parallel to T_1 (for a review, see also Marois & Ivanoff, 2005).

3.2.3 Dual-process models

Two conclusions can be drawn from the two previous sections. First, the central bottleneck model has received a vast amount of support. Secondly, the assumption of a gradually allocated central resource is thus far not very well supported. However, there are results that seriously pose challenges to the central bottleneck model. As illustrated in Figure 3.3 the original model (e.g., Pashler, 1994) assumes strict seriality. Hence, findings that RT_1 is modulated by any correspondance of T_1 and T_2 (although R_1 is given well before R_2) are difficult to reconcile with this model. For example, in a study by Hommel (1998), participants responded with a key press to a red or green rectangle in T_1, and by uttering "red" or "green" in response to the letters 'S' and 'H' in T_2. Contrary to what a strictly serial model would predict, RT_1 was (at short SOAs) 28ms faster when S_1 and R_2 dimensionally overlapped (e.g., S_1 was a green rectangle and R_2 was "green"). Such *backward correspondance* or *crosstalk effects* have subsequently been replicated with other tasks and varying response modalities (see, e.g., Hommel & Eglau, 2002; Koch, 2008; Miller, 2006), even for task-irrelevant characteristics of T_2 (Lien & Proctor, 2000).

To explain such backward correspondance effects, Hommel (1998) and Lien and Proctor (2002) suggested to subdivide the central stage into two sub-stages. (1) Immediately after a stimulus has been processed the stage of *stimulus-response translation* begins and runs in parallel to other stages. This stage automatically activates possible responses, and if (likely with short SOAs) two such stages overlap in time, the mutual interference or facilitation occurs. (2) Then a bottleneck stage of *final response selection* follows to finally activate the desired response above threshold. It is this second substage that cannot be bypassed and that produces the PRP effect. Converging evidence comes from an electrophysiological study using the lateralized readiness potential, showing that T_2 response activation coincides in time with central processing of T_1 (Lien, Ruthruff, Hsieh & Yu, 2007). In sum, such models can potentially explain the typical PRP effect, but also can account for correspondance/crosstalk effects, which suggest that at least some parts of response selection occur in parallel.

3.2.4 Evaluation of current models

In the previous sections I have reviewed various theoretical accounts for the PRP effect. On one side, the (structural) central bottleneck model has thus far stimulated most of the research and has received a great amount of empirical evidence. On the other side, in particular formalized models of graded capacity sharing (Tombu & Jolicoeur, 2003) represent an interesting and viable alternative, under which the central bottleneck model can be subsumed as a special case. Dual-process models (Hommel, 1998; Lien & Proctor, 2002) have the potential to explain PRP effects plus signs of some parallel processing.

At present, however, given the rather limited evidence for graded capacity sharing and strategic deferments plus the additional behavorial, electrophysiological, and neuroimaging evidence supporting a structural bottleneck, I currently favor the (structural) central bottleneck model as illustrated in Figure 3.3. Thus, this model will be underlying the later reported experiments, although the reported data will also be interpreted with regards to alternative models where necessary.

3.3 Localization of experimental factors

Both the central bottleneck model (see Section 3.2.1) and dual-process models (see Section 3.2.3) allow for specific predictions concerning the exact time course and the nature of dual-task interference. In addition, procedures have been developed to locate the origins of effects (expressed as RT differences between two or more levels of an experimental factor) relative to the (central) bottleneck stage. Although this is not the present work's main purpose, the use of Garner-Interference in T_2 allows for such localization. I will now continue with a brief description of the two most relevant procedures. Both procedures have been used often in the literature and are quite established (e.g., Ferreira & Pashler, 2002; Miller & Reynolds, 2003; Paelecke & Kunde, 2007). More detailed descriptions are given by Pashler and Johnston (1998) or Miller and Reynolds (2003), and see also Appendix A.

3.3.1 The locus-of-slack procedure

In this often used procedure the manipulation of interest is implemented in T_2 and this procedure is used to determine whether an effect arises (1) at the pre-central stage, or (2) at the central or post-central stage. The critical result is the interaction of the implemented effect with the dual-task factor SOA. In the first case both should combine underadditively, i.e., at short SOAs the effect should be reduced or even absent. This is so, because the prolongation of the pre-central stage in T_2 is absorped into the cognitive slack (e.g., Schweickert, 1978). In the second case, the interaction should be additive since prolonging central or post-central stages of T_2 affects RT_2 to the same degree across all SOA levels.

3.3.2 The effect-propagation procedure

If the locus-of-slack procedure yields an additive interaction of SOA and the effect of interest, this additivity may be due to prolongation of the central stage or the post-central stage. In a sense, the effect-propagation procedure provides the complementary information and allows for deciding whether the effect arises at (1) the pre-central or central stage or at (2) the post-central stage. Now the manipulation is implemented in T_1. In the first case, the effect should be evident (at short SOAs) in both T_1 and T_2 to the same extent. In other words, the effect implemented in T_1 is propagated into T_2 (or RT_2). In the second case, the effect should be absent in T_2.

3.4 Chapter summary

In this chapter I have introduced the PRP paradigm as a methodological tool for analyzing dual-task interference. This interference becomes apparent in slowed RT_2 at short SOAs – the PRP effect. Of the various proposed accounts, the central bottleneck model (Pashler, 1994; Pashler & Johnston, 1998; Welford, 1952) has received wide empirical support and underlies the present work. I will now continue by giving an overview of the purposes of this present study and the experiments I will report on.

4 The present study

The following two Chapters 5 and 6 are the empirical part of the present work. Seven experiments are subdivided into two series of three and four experiments, respectively.

- **Series I: Does dorsal processing require central capacity?**

  Experiments 1-3 adress the question of whether dorsal processing (in the present case: right-handed precision grasping) requires central capacity or can be construed as automatic (see Section 2.5). Given the ambiguous conclusions from recent studies plus possible alternative accounts for the PRP effect in the Kunde et al. (2007) study, I here pursue the PRP paradigm and attempt to rule out these alternative accounts. To resolve this issue is important for at least three reasons. First, knowing in which respects processing in the ventral and dorsal streams differ (and in which respects they do not) will generally help to elaborate the Action-Perception Model. Secondly, this question is also important from the perspective of dual-task research. The PRP effect has been shown to be very robust across a variety of tasks, and only few exceptions were reported (Lien et al., 2006). One potential exception made use of eye-movements as responses - a response mode perhaps controlled by specific neural circuits (Pashler et al., 1993). In light of these results, dorsally mediated grasping movements may indeed be a good candidate for another exception, and thus their sensitivity to dual-task interference deserves thorough experimental investigation. Third, knowing the capacity-limitations of a typical dorsal task may also have implications for Human Factors research. After all, object-oriented tasks such as grasping or pointing (either directly or even mediated by a tool) are part of many working environments. It is clearly important to know whether other concurrent tasks (such as verbal communication) do interfere with, or are affected themselves, by apparently simple dorsal motor tasks.

  As repeatedly mentioned, the validity of using visual illusory effects to identify the underlying (ventral or dorsal) processing mode is discussed rather controversial (Franz & Gegenfurtner, 2008; Goodale, 2008). Garner-Interference might be a promising alternative, but has to date not often been used in experimental investigations of the Action-Perception Model. Therefore, an additional purpose of Experiment 1 was to replicate Garner-Interference for a ventral task in a PRP setting, as was reported earlier by Kunde et al. (2007). Replicating this dissociation appears important to me in order to make this method more convincing. In turn, this would be a good starting position for (in particular) Experiments 4-7 that use Garner-Interference to identify possible contributions from the ventral stream to particular grasping movements.

- **Series II: Do left-handed and/or unskilled grasps escape dorsal processing?**

  The initial formulation of the Action-Perception Model already suggested that not all actions are mediated by the dorsal stream. In particular, all actions for which visual input is not immediately available were suggested to be based on the perceptual representations provided by the ventral stream (Goodale et al., 1994, 2004). Recently, however, it was suggested that also left-handed and unskilled grasping relies on such perceptual information (Gonzalez et al., 2006, 2008). As here visual input is available when such movements are initiated, these suggestions are a step away from the initial formulation of the Action-Perception Model. However, these latter suggestions were solely based on an effect of visual illusions on the grasping movements. From the discussion in Section 2.3 it should be clear though, that such findings must therefore be interpreted with caution. In Experiments 4-7 I approach this topic by using Garner-Interference to assess a possible ventral contribution to left-handed and unskilled grasping.

  Experiments 4, 5, and 7 were run as PRP experiments for better comparability with Experiments 1-3; Experiment 6 assesses unskilled grasping in a single-task context.

As most of the experiments (except for Experiment 6) are settled within the PRP paradigm (see Section 3.1), a detailed method description will be given only for Experiment 1. For the remaining experiments I will only introduce deviations from Experiment 1.

Following each series of experiments, I will provide a comprehensive discussion. The main results and conclusions from both experimental series will then briefly be reiterated in the General Discussion and subsequently be evaluated against the background of the Action-Perception Model and PRP/dual-task research (Chapter 7).

5 Experiments 1-3: Does dorsal processing require central capacity?

In Section 2.5 I have discussed the few recent studies on whether dorsal processing requires central capacity. These studies left an ambigious picture: some authors concluded positive, yet others negative. One of these former authors are Kunde et al. (2007), who used the perceptual judgment and the grasping task of Ganel and Goodale (2003) as T_2 in a PRP experiment. The results of this study are visualized in Figure 5.1, and three results are notable. First, Garner-Interference (see Section 2.6) ocurred in the perceptual judgment, but not in the grasping task. Thus, the results of Ganel and Goodale (2003) replicate even in a dual-task setting. Secondly, Garner-Interference combined additively with SOA, suggesting the implication of central instead of (perceptual) pre-central stages. Thirdly, a PRP effect of roughly the same size was found for both tasks, suggesting that grasping is *not* automatic and effortless. However, on closer inspection the findings of Kunde et al. (2007) may portray an incorrect picture. In particular the PRP effect may also have arisen (1) from strategically withholding the grasping movement in order to comply with the instructions or (2) from peripheral interference due to an overlap in response modalities. These arguments will be outlined in more detail below.

The following Experiments 1-3 attempt at clearly showing whether or not a PRP effect arises for skilled right-handed precision grasping. Despite the mere theoretical interest for this, this becomes also important for the later Experiments 4-7, where other types of grasping (left-handed and unskilled grasping) are investigated in a dual-task setting. It might still be possible that skilled right-handed, but not other types of grasping, are free from dual-task interference.

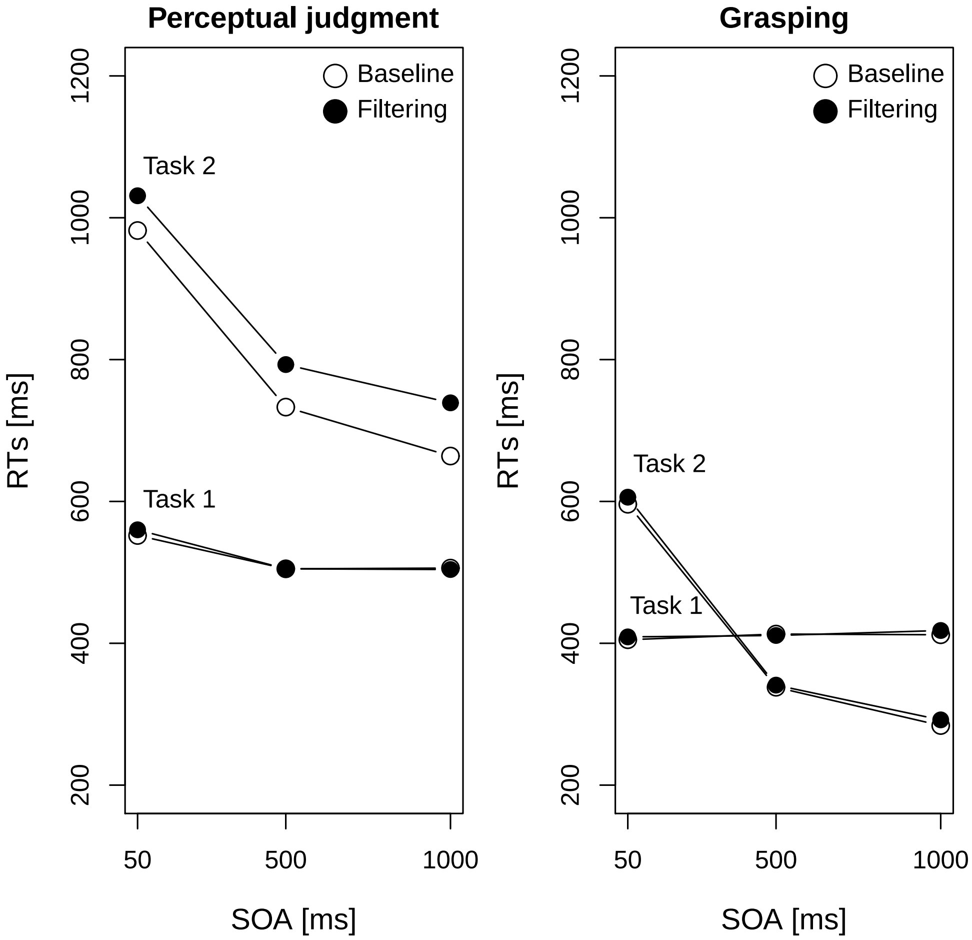


Figure 5.1: Replotted response times (RT) in milliseconds from the Kunde et al. (2007) study as a function of condition and stimulus onset asynchrony (SOA). Left panel: perceptual judgment as Task 2, right panel: grasping as Task 2.

5.1 Experiment 1

In a previous study (Kunde et al., 2007) that combined a binary choice reaction task (tone discrimination) as T_1 with a dorsal grasping task as T_2 in a PRP paradigm, mean RT_1 was roughly 400ms. Critically, mean RT_2 in the grasping task was only about 300ms at an SOA of 1000ms, i.e., without considerable task overlap (see Figure 5.1). Therefore, in principle grasping could have been performed faster than T_1 at the shortest SOA of 50ms, at least in the majority of trials. Yet, having been instructed to respond in task order and to focus on T_1 performance, the participants were obliged to strategically withhold grasping until after R_1 was given in order to not commit an error. This in turn could have produced the observed PRP effect. The present Experiment 1 closely followed the study by Kunde et al. (2007), but importantly, the instructions placed equal emphasis on both tasks and grasping ahead of R_1 was not counted as erroneous (for a similar approach see Experiment 1 of Ruthruff et al., 1995). The important question was whether the abandonment of a certain task order would remove the PRP effect for the dorsal grasping task. In addition, I expected to replicate the presence of Garner-Interference with the perceptual judgment task and the lack thereof with the grasping task. This would be the third independent study, and a successful replication renders Garner-Interference a more convincing indicator of ventral processing.

5.1.1 Method

Participants

Sixteen undergraduate students from Dortmund University of Technology (3 male, mean age = 22;8 years) participated in return of course credit.

Design, apparatus, and stimuli

Each participant performed in two sessions of a PRP experiment. In both sessions, T_1 was a binary tone classification task with a left hand key press as R_1. Stimuli were 300 and 900 Hz tones (50ms) presented via headphones. T_2 was either a grasping or a perceptual judgment task, varying across both sessions. Both tasks were modeled after Ganel and Goodale (2003): in the grasping task, participants naturally grasped a stimulus across its width with their right hand using a precision grip; in the perceptual judgment task, they indicated the same stimuli' width with a right hand key press. Stimuli were four wooden white-colored blocks constructed according to a factorial combination of their width (30 and 35.7mm) and length (63 and 75mm) (see also Figure 2.3 and Felfoldy (1974) and Ganel and Goodale (2003)). Participants wore computer-controlled PLATO shutter glasses (Translucent Technologies; Milgram, 1987) during the experiment, and the stimuli were presented on a small custom-made table where they depressed a hidden micro switch. RT_1 was measured from tone presentation until the left hand response, RT_2 from the shutter glasses opening until the right hands response (perceptual judgment) or until the participants right index finger left a home button (grasping). For the grasping task, movement time (MT) was additionally measured from the finger's leaving the home button until lifting the stimulus object.

Procedure

Each participant performed in four experimental blocks[1] of 72 trials each. Two blocks were baseline conditions in which only the two stimulus objects of the same length were used, the remaining blocks were filtering conditions and used all four stimulus blocks. Prior to each experimental block, participants were shown those stimulus blocks that were used in the upcoming experimental block. Four experimental block orders were applied resulting from counterbalancing the two possible baseline conditions and two filtering conditions, with the order of the two possible baseline conditions also counterbalanced. The experimental blocks were preceded by an unanalyzed practice block of 24 trials. Each trial began with a short warning click after which S_1 (the auditory stimulus in T_1) was presented. Following a varying SOA of 50, 500, or 1000ms, the shutter glasses opened and provided view of the stimulus block (see Figure 5.2 for an illustration of a trial's time-course). All T_1 errors and T_2 perceptual judgment errors were detected automatically, T_2 grasping accuracy was judged by the experimenter: a grasp was only judged correct if a precision grip was used. The experimenter gave feedback after each trial. Then, the shutter glasses became opaque again and the experimenter prepared and initiated the next trial. Instructions placed equal emphasis on both tasks allowing the participants to respond in whatever order they want to, as long as they responded as fast and accurate as possible.

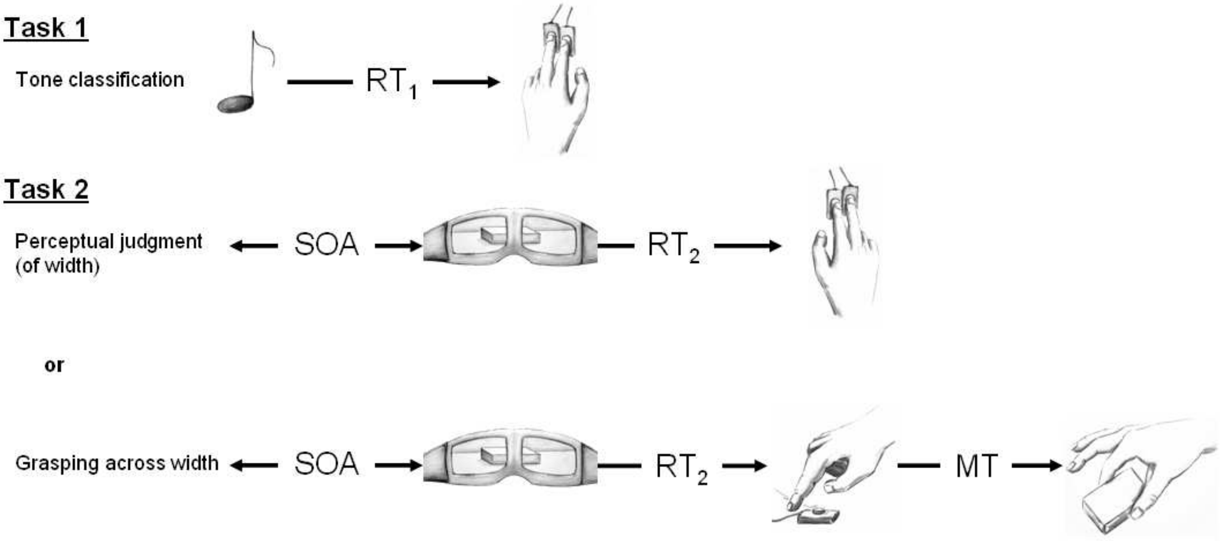


Figure 5.2: Illustration of a trial's time course in Experiment 1 (SOA = stimulus onset asynchrony; RT = response time; MT = movement time).

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[1] To disambiguate I refer the to-be-grasped stimuli to as 'stimulus blocks' and the experimental blocks of trials to as 'experimental blocks' or 'conditions' in the remainder of this work.

Data treatment and analyses

Analyses were mainly done by means of analysis of variance (ANOVA) with the factors 'condition' (baseline *vs.* filltering) and SOA (50 *vs.* 500 *vs.* 1000ms) as repeated measures. Mauchly's test was used to assess violations of the sphericity assumption. In this case, the corresponding Greenhouse-Geisser ϵ is reported (Greenhouse & Geisser, 1959) and appropriate corrections were applied. For easier communication, however, I report uncorrected degrees of freedom. Further additional analyses I will introduce where necessary in the respective results section. Analyses and result plotting were mainly done using the R-software (R Development Core Team, 2009).

Trials with general errors (e.g., no response within 4sec., R_2 given before S_2 onset, ...) were excluded right out. Error analyses are based on the remaining trials with T_1 and T_2 mean error percentages as the dependent measures. For RT (and MT) analyses, only those trials were further considered where both R_1 and R_2 were correct. RTs less than 150ms and RTs exceeding the individual's mean by more than 2.5 individual standard deviations (calculated separately for each participant and analyzed condition) were identified as outliers (and were excluded for RT and MT analyses). With grasping as T_2, 2.7% and 4.4% of the trials in T_1 and T_2 were excluded as outliers; the corresponding values for perceptual judgment as T_2 are 2.6% and 2.3%.

For all analyses an α-level of .05 was adopted, and sample effect sizes are reported as partial η^2 (η^2_P). Visualizations of RT and MT data are supported by 95% within-subject confidence intervals according to Loftus and Masson (1994).

5.1.2 Results

RT and MT analyses

- **Perceptual judgment as T_2**

  Mean RTs are illustrated in Figure 5.3a (for details see Table B.1). On a descriptive level, mean RT_1 was slightly longer in the filtering than in the baseline condition, but roughly on one level across all SOA values. Neither the two main effects were significant; SOA: $F(2,30) = 1.04$, $p = .34$, $\eta^2_P = .07$, $\epsilon = .68$; condition: $F(1,15) = 0.84$, $p = .38$, $\eta^2_P = .05$; nor was the interaction; $F(2,30) = 0.91$, $p = .36$, $\eta^2_P = .06$, $\epsilon = 56$. Mean RT_2 was longer in the filtering than in the baseline condition and exhibited a large decrease with increasing SOA. Accordingly, the main effects were significant; $SOA: F(2,30) = 119.5$, $p < .01$, $\eta^2_P = .89$, $\epsilon = .56$; condition: $F(1,15) = 5.51$,

$p < .05$, $\eta_P^2 = .27$; but the interaction not; $F(2, 30) = 1.63$, $p = .22$, $\eta_P^2 = .10$, $\epsilon = 73$. Repeated contrasts on the factor SOA showed a significant decrease in RT_2 from SOA = 50ms to SOA = 500ms; $F(1, 15) = 161.88$, $p < .01$, $\eta_P^2 = .92$; as well as from SOA = 500 to SOA = 1000 ms; $F(1, 15) = 39.08$, $p < .01$, $\eta_P^2 = .72$.

- **Grasping as T_2**

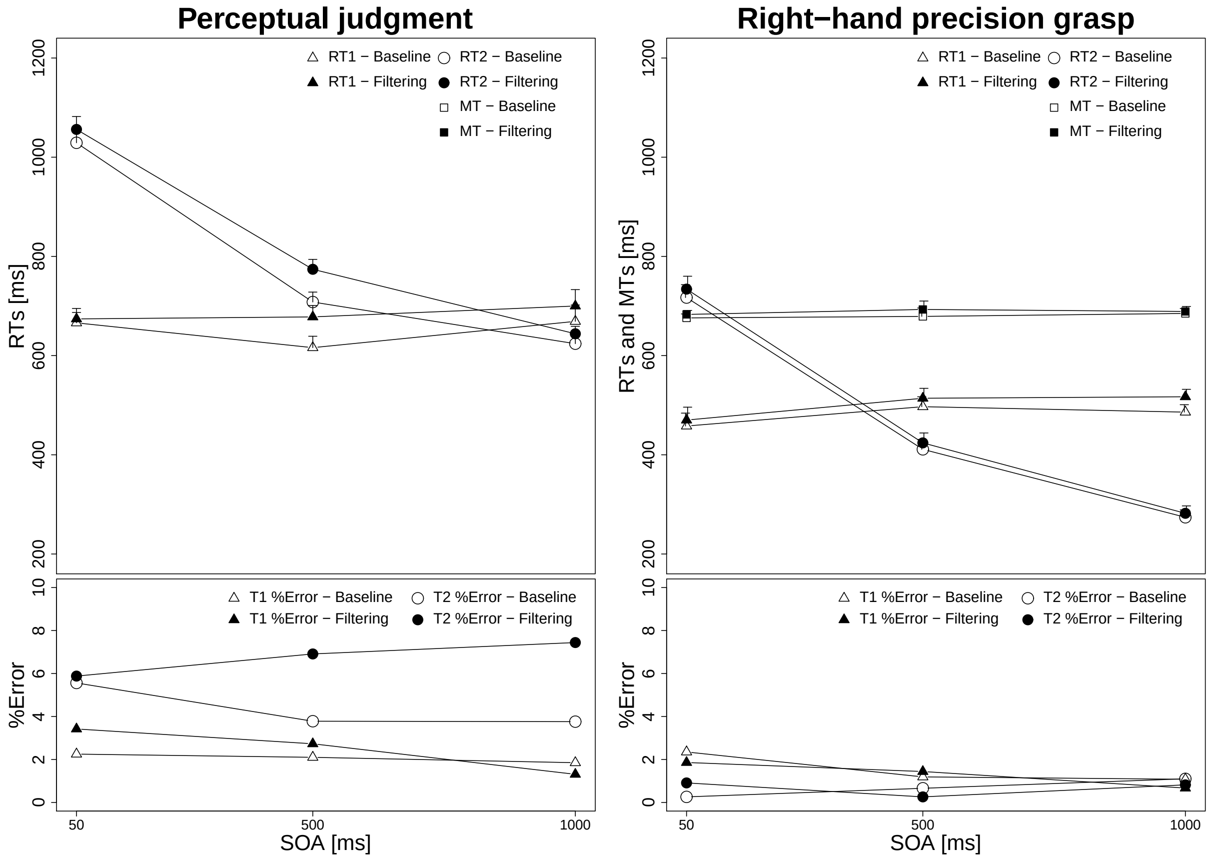
  Mean *RT*s and *MT*s are visualized in Figure 5.3b (for details see Table B.1). Mean RT_1 was slightly longer in the filtering condition compared to the baseline condition and seemed to increase with an increasing SOA. The latter was confirmed by a significant main effect SOA; $F(2, 30) = 8.38$, $p < .01$, $\eta_P^2 = .36$, $\epsilon = .65$. No other effect was significant; condition: $F(1, 15) = 2.05$, $p = .17$, $\eta_P^2 = .12$; SOA × condition: $F(2, 30) = 0.71$, $p = .50$, $\eta_P^2 = .12$.

  Mean RT_2 was again slightly longer in the filtering condition than in the baseline condition, and largely decreased with an increasing SOA. While the latter aspect is supported by a significant effect of SOA; $F(2, 30) = 206.10$, $p < .01$, $\eta_P^2 = .93$, $\epsilon = .62$; the difference between conditions was not reliable; $F(1, 15) = 1.20$, $p = .29$, $\eta_P^2 = .07$; as neither was the interaction; $F(2, 30) = 0.26$, $p = .77$, $\eta_P^2 = .02$. Repeated contrasts on the factor SOA showed a significant decrease in RT_2 from SOA = 50ms to SOA = 500ms; $F(1, 15) = 231.59$, $p < .01$, $\eta_P^2 = .94$; as well as from SOA = 500ms to SOA = 1000ms; $F(1, 15) = 87.39$, $p < .01$, $\eta_P^2 = .85$. There were no reliable effects on *MT*s (all p's$> .2$).

In general, *RT*s were higher with perceptual judgment than with grasping as T_2. Mean RT_1 were 491 and 668ms (for grasping and perceptual judgment as T_2, respectively); $F(1, 15) = 11.44$, $p < .01$, $\eta_P^2 = .43$. The respective mean RT_2 were 479 and 805ms; $F(1, 15) = 45.40$, $p < .01$, $\eta_P^2 = .75$

Error analyses

Mean percentages of errors are visualized in Figure 5.3 (for details see Table B.2). With perceptual judgment as T_2, there were two significant effects. First, error rates in T_1 decreased with an increasing SOA; $F(2, 30) = 3.82$, $p < .05$, $\eta_P^2 = .20$. Secondly, in T_2, error rates decreased with an increasing SOA in the baseline condition, but the opposite was true for the filtering condition. Accordingly, the interaction of SOA and condition



(a) (b)

Figure 5.3: Mean response times (*RT*) and movement times (*MT*) in milliseconds, and mean error percentages (%Error) from Experiment 1 as a function of stimulus onset asynchrony (SOA) and condition. (a) Perceptual judgment as T_2; (b) Grasping as T_2. Error bars are 95% within-subject confidence intervals according to Loftus and Masson (1994), calculated across the factor condition.

was significant; $F(2, 30) = 4.33$, $p < .05$, $\eta_P^2 = .22$. With grasping as T_2, the analyses uncovered only one marginally significant effect suggesting decreasing error rates in T_1 with an increasing SOA; $F(2, 30) = 3.20$, $p = .06$, $\eta_P^2 = .18$. No other effects were reliable (all p's$> .1$).

5.1.3 Discussion

In Experiment 1, participants took part in a PRP experiment with either grasping (conceived as a dorsal task) or a perceptual judgment (conceived as a ventral task; see also Ganel & Goodale, 2003) as T_2. One goal of Experiment 1 was to test whether the PRP effect on grasping observed by Kunde et al. (2007) was due to the instructions focusing on T_1 performance, rather than the existence of a central processing stage in grasping. My approach was to re-run the original study with altered instructions placing equal emphasis on both tasks and allowing a freely chosen response order (see also Ruthruff et al., 1995).

Despite the altered instructions and some minor differences of mostly technical nature, there is a remarkable amount of commonalities with the results observed by Kunde et al. (2007). With the perceptual judgment as T_2, there was clear evidence of a PRP effect for RT_2, and additionally Garner-Interference (i.e., the fact that the filtering condition caused longer RTs than the baseline condition did; Ganel & Goodale, 2003), was additive with the SOA. Of more importance are the results related to grasping as T_2. The non-significant Garner-Interference suggests a dorsal mode of processing (Ganel & Goodale, 2003), but despite the altered instructions, I observed a large PRP effect. In addition, the results showed a significant RT_2 decrease from SOA = 500ms to SOA = 1000ms. At the 500ms SOA, however, no need arises to strategically defer R_2 and the observed further decrease adds evidence against the alternative account advanced in the introduction to Experiment 1. Somewhat unexpected is the increase of RT_1 with an increasing SOA. This is neither predicted by the central bottleneck model (predicting no effect on RT_1 at all; Pashler, 1994) nor by capacity sharing models (predicting decreasing RT_1 with increasing SOA; Tombu & Jolicoeur, 2003). I see two potential reasons for this. First, with the altered instructions, participants may have tended to group their responses (i.e., to respond more or less simultaneously to both tasks). However, the effect of SOA on RT_1 remains significant even after excluding trials with an IRI less than 50ms (Miller & Ulrich, 2008); $F(2, 30) = 4.00$, $p < .05$, $\eta_P^2 = .21$. Secondly, unlike RT_1, the mean error percentages in T_1 decreased with increasing SOA. This specific feature of the results might thus be due to a speed-accuracy trade-off. Yet, because the effects of theoretical interest occur in T_2, and are probably unaffected by this T_1 outcome, I refrain from going into detail on this issue.

A note of caution need to be articulated here. If 'T_2 task' (grasping *vs.* perceptual judgment) is added as an additional repeated measure into the analyses it fails to enter into a significant interaction task × condition. This particular drawback may be seen negative since it indicates that the numerical amount of Garner-Interference did not differ between both tasks (see already Cantor, 1956). To anticipate, in Experiment 7 the interaction was clearly present. As a side note: the same problem applies, e.g, to the study by Hu and Goodale (2000). These authors found a larger illusion effect with delayed grasping than with normal grasping, but never tested whether this difference was significant at all.

Re-analyses showed that this is not the case (see, e.g., Franz & Gegenfurtner, 2008).

Finally, an important and crucial question is: did the participants accept the invitation to reverse their response orders, i.e., were the altered instructions successful? The data show that participants mostly did not. In fact, except for one, all participants almost always responded to T_1 before leaving the home button. The one exceptional participant is quite informative nevertheless, because she showed response reversals in 67, 36, and 12% of the trials (for the SOA conditions of 50, 500, and 1000ms, respectively). Thus, in principle response reversals were possible under these experimental conditions. Moreover, treating the trials from this participant as independent observations revealed a significant PRP effect: RT_2 significantly dropped from 726 to 347ms over the full SOA range; $F(2, 274) = 38.23$, $p < .01$, $\eta_P^2 = .24$. Unfortunately, it is impossible to tell from my data whether the other participants were unable to reverse their response order or simply chose not to do so. Experiment 2 was run to more convincingly demonstrate response reversals but a persisting PRP effect.

5.2 Experiment 2

The large PRP effect in dorsal tasks (Kunde et al., 2007) can potentially be attributed to strategic T_2 deferments. To rule out this explanation, in Experiment 1 the participants were free to choose any response order they want to - a method that has been used earlier in PRP research (Ruthruff et al., 1995). Despite this altered instructions, I replicated the large PRP effect. Admittedly, however, only very rarely did the participants reverse their response order, leaving open whether or not the instructions were powerful enough to successfully rule out the abovementioned alternative account. In Experiment 2, I thus attempted to further stimulate parallel processing but still to provide evidence for a remaining PRP effect under these conditions. One largely uncontroversial exception from the PRP effect appear to be saccadic eye movements as R_2 (Pashler et al., 1993). In this study, on some trials, a negative SOA was used, i.e., S_2 appeared before (rather than after) S_1. This manipulation was introduced to prevent participants from adopting an obvious response order (e.g., always respond first to T_1, then to T_2). In addition, parallel processing is induced when short SOAs occur more frequently than long SOAs (Miller, Ulrich & Rolke, 2009). To maximize efforts, I combined both methods in Experiment 2: (1) I used negative SOAs and (2) the shortest SOAs (-50 and 50ms) were thrice as frequent as the other SOAs were. Finding both response reversals and the PRP effect in the dorsal grasping task would be a strong empirical argument against the strategic deferment hypothesis and the remaining reservations concerning Experiment 1.

5.2.1 Method

Participants

Eight new undergraduate students from Dortmund University of Technology (1 male, mean age = 23;0 years) participated in return of course credit.

Design, apparatus, stimuli, and procedure

For the most parts, this experiment resembles Experiment 1 with three differences. First, participants took only part in one single session of a PRP experiment with the grasping task as T_2. Secondly, I did not distinguish between baseline and filtering conditions, but all four possible stimulus objects were used throughout all experimental blocks. The third change concerns the SOA manipulation. In the present experiment, I used SOAs of -150, -50, 50, 150, 250, and 500ms. A negative SOA means that S_2 was presented before (rather than after) S_1 (see Pashler et al., 1993). In addition, the frequency of the two shortest SOAs (-50 and 50ms) was thrice higher (24 times each) than the frequency of the other SOAs was (eight times each) to further stimulate parallel processing (Miller et al., 2009). The experiment was divided into four experimental blocks of 80 trials each. The experimental blocks were preceded by an unanalyzed practice block of 22 trials. The instructions were similar to those in the Pashler et al. (1993) study and focused on speed while not giving priority to one task over the other or suggesting a preferred response order. Also similar to this study, no feedback was given to the participants.

The stimulus-response mapping of T_1 was counterbalanced across participants, and the eight possible combinations of S_1 (low *vs.* high tone) and S_2 (four T_2 stimulus blocks) occurred equally often at each SOA level in a random order.

Data treatment and analyses

Analyses were done by means of ANOVA with the factor SOA (-150 vs. -50 vs. 50 vs. 150 vs. 250 vs. 500ms) as a repeated measure. 2.3% and 5.1% of the trials were excluded as outliers in T_1 and T_2, respectively.

5.2.2 Results

In a first step, I assessed whether participants did vary their response order. Across the six SOA conditions, participants left the home button before they responded to the tone classification task in 77.0, 74.4, 73.2, 70.8, 65.3, and 36.8% of the trials. Clearly, the manipulations introduced in this experiment were successful in preventing participants from adopting a particular response order. Hence I went on to analyze the RT/MT and error data in a second step.

RT and MT analyses

Mean RTs and MTs are illustrated in Figure 5.4. RT_1 showed an increase of 66ms across the six SOA conditions (645, 625, 635, 667, 675, and 711ms). At the same time, RT_2 showed a large decrease of 266 ms (543, 487, 436, 381, 336, and 277ms). SOA had a significant effect in both tasks; T_1: $F(5,35) = 4.85$, $p < .01$, $\eta_P^2 = .41$; T_2: $F(5,35) = 23.10$, $p < .01$, $\eta_P^2 = .77$, $\epsilon = .29$. MTs remained almost constant (varying from 586 to 595ms), and the effect of SOA was not significant; $F(5,35) = 0.33$, $p = .70$, $\eta_P^2 = .05$, $\epsilon = .36$.

Error analyses

Mean error percentage (see Figure 5.4) in T_1 decreased slightly across the SOA conditions (11.1, 7.5, 6.8, 3.9, 2.7, and 4.5), and the effect of SOA was significant; $F(5,35) = 4.07$, $p < .05$, $\eta_P^2 = .37$, $\epsilon = .36$. On the descriptive level, the same pattern was found for mean error percentage in T_2 (2.8, 2.5, 1.7, 1.2, 2.0, and 0.8), but the effect of SOA was not significant; $F(5,35) = 1.02$, $p = .42$, $\eta_P^2 = .13$.

5.2.3 Discussion

In Experiment 2, I maximized efforts to induce parallel processing of the tone classification task and the grasping task in a PRP experiment. This was done to unambiguously rule out strategic T_2 deferment as the source of the PRP effect reported by Kunde et al. (2007) and also in my Experiment 1. To this end, I modified the standard PRP paradigm by adding two manipulations, namely, negative SOAs where S_2 occurred prior to S_1 (Pashler et al., 1993), and a larger likelihood of short SOAs, what induces a shift from serial to parallel processing (Miller et al., 2009). The results of this Experiment 2 are straightforward: although participants reversed their response order on the majority of the trials, the results are qualitatively similar to those of Experiment 1. In particular, RT_1 showed a slight increase with an increasing SOA (I again suspect this in parts being due to a speed-accuracy trade-off).

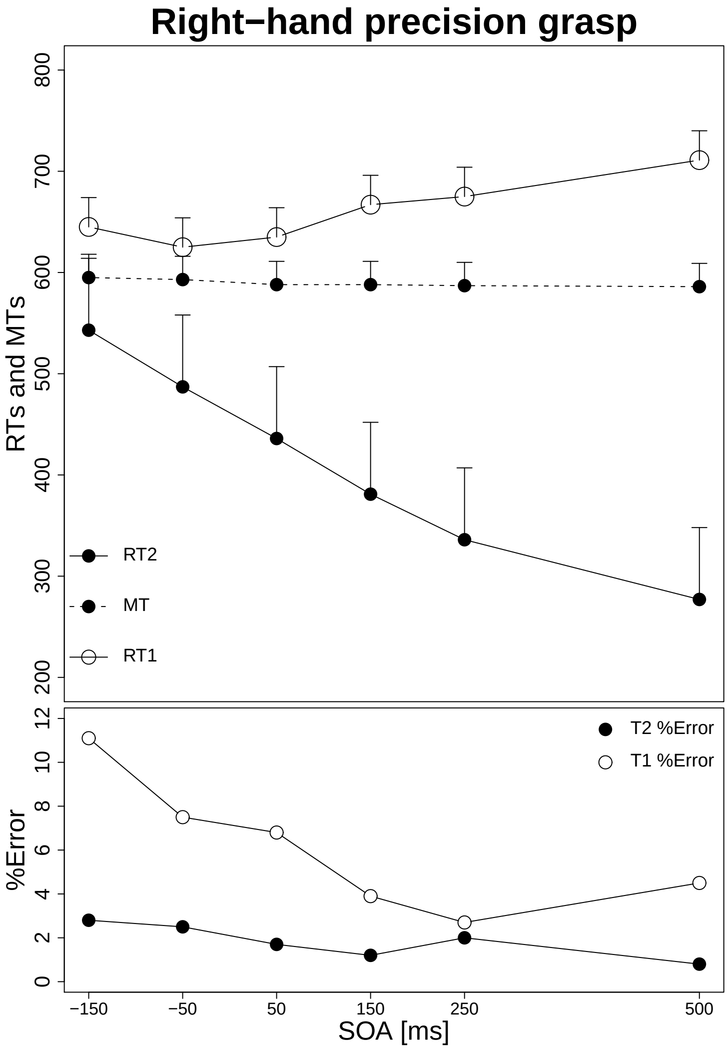


Figure 5.4: Mean response times (RT) and movement times (MT) in milliseconds, and mean error percentages (%Error) from Experiment 2 as a function of stimulus onset asynchrony (SOA). Error bars are 95% within-subject confidence intervals according to Loftus and Masson (1994).

Contrary to that, RT_2 exhibited the typical PRP effect, as indicated by a sharp decrease of 266ms with an increasing SOA - more than twice as big as the one reported by Pashler et al. (1993). Note that even the RT_2 decrease from the SOA of 50ms to the SOA of 500ms was 159ms, which is more than thrice as much as the comparable effect in the Pashler et al. (1993) study. In sum, Experiments 1 and 2 suggest that a typical dorsal grasping task is subject to massive interference from a concurrent choice reaction task, even when participants can perform the two tasks in any order they desire. This renders it unlikely that previous observations of PRP effects in dorsal tasks are due to a strategic T_2 deferment required to maintain a specific (instructed) task and response order. Experiment 3 aims at ruling out a second alternative account based on response modality related interference between both tasks.

5.3 Experiment 3

Dual-task interference also can ensue for other reasons than central capacity limitations. One such reason is peripheral output interference. For example, shaving and tooth brushing are two tasks that essentially cannot be performed simultaneously since they (at least in the majority of cases) require the same effector (most often the right hand). A similar though more moderate argument may apply to earlier PRP studies with grasping as the secondary task as well. The responses in both tasks were manual: a key press in the tone classification task and a grasping movement in the grasping task (or another key press in the perceptual judgment task). One might argue that the observed interference was simply due to the identical response modalities. It is well known that producing responses with both hands at the same time affects performance adversely (e.g., Heuer, 1995), what is known as bimanual interference. A related, but more general, objection can be derived from multiple resource theories (see, e.g., Navon, 1984; Wickens, 1980, 1984) suggesting that the amount of interference relates somehow to the joint competition for specific resource pools. In fact, PRP experiments with two manual responses appear to produce larger dual-task costs than those with differing response modalities (Pashler, 1990; Ruthruff et al., 2001). To circumvent such response modality-related accounts, I ran the grasping condition from Experiment 1 again, but replaced the manual key press response in the tone classification task with a vocal response. The resulting task pairing (auditory-vocal/visual-manual) is also on par with what Hazeltine, Ruthruff and Remington (2006) have termed a standard pairing, assumed to favor parallel performance of two tasks.

5.3.1 Method

Participants

Sixteen new undergraduate students from Dortmund University of Technology (3 male, mean age = 23;8 years) participated in return of course credit.

Design, apparatus, stimuli, and procedure, data treatment and analyses

In most parts, Experiment 3 resembles Experiment 1, but participants took only part in one single session where grasping was T_2 in a PRP experiment. Two other exceptions apply. First, the participants responded to S_1 in the tone classification task with uttering either "tip" or "top". *RT*s in this task were measured by means of a voice key, and the type of the responses was recorded by the experimenter. Secondly, the instructions focused on T_1 and emphasized speed and accuracy. In all other respects, Experiment 3 was similar to the grasping task as described for Experiment 1. 2.0% and 4.3% of the trials were excluded as outliers in T_1 and T_2, respectively.

5.3.2 Results

RT and MT analyses

Mean *RT*s and *MT*s are visualized in Figure 5.5 (for details see Table B.3). Similar to Experiment 1, mean RT_1 was slightly longer in the filtering condition compared to the baseline condition and increased with an increasing SOA. The latter finding was confirmed by a significant main effect of SOA; $F(2,30) = 15.61$, $p < .01$, $\eta_P^2 = .51$. No other effect was significant; condition: $F(1,15) = 1.63$, $p = .22$, $\eta_P^2 = .10$; SOA × condition: $F(2,30) = 2.02$, $p = .15$, $\eta_P^2 = .12$.

Of main interest here is that mean RT_2 showed, again, a large decrease with an increasing SOA, supported by a significant effect of SOA; $F(2,30) = 284.24$, $p < .01$, $\eta_P^2 = .95$, $\epsilon = .60$. Neither the difference between conditions was reliable; $F(1,15) = 2.04$, $p = 17$, $\eta_P^2 = .12$; nor was the interaction; $F(2,30) = 2.74$, $p = .08$, $\eta_P^2 = .15$. Repeated contrasts on the factor SOA support a significant decrease in RT_2 from SOA = 50ms to SOA = 500ms; $F(1,15) = 635.34$, $p < .01$, $\eta_P^2 = .98$; as well as from SOA = 500ms to SOA = 1000ms; $F(1,15) = 82.93$, $p < .01$, $\eta_P^2 = .85$. Unexpectedly, the mean *MT*s also increased slightly with an increasing SOA; $F(2,30) = 25.41$, $p < .01$, $\eta_P^2 = .63$. No other effect was significant; condition: $F(1,15) = 0.64$, $p = .44$, $\eta_P^2 = .04$; SOA × condition: $F(2,30) = 2.60$, $p = .09$, $\eta_P^2 = .15$.

Error analyses

Mean percentages of errors are visualized in Figure 5.5 (for details see Table B.3). There were two significant effects. First, and similar to Experiment 1, mean error percentage in T_1 decreased with an increasing SOA; $F(2,30) = 3.98$, $p < .05$, $\eta_P^2 = .21$, $\epsilon = .72$.

Secondly, in T_2, mean error percentages decreased with an increasing SOA in the baseline condition, and slightly increased (at least from SOA = 50ms to SOA = 1000ms) in the filtering condition, resulting in a significant interaction; $F(2, 30) = 4.47$, $p < .05$, $\eta_P^2 = .23$. No other effects were reliable (all p's $\geq .24$).

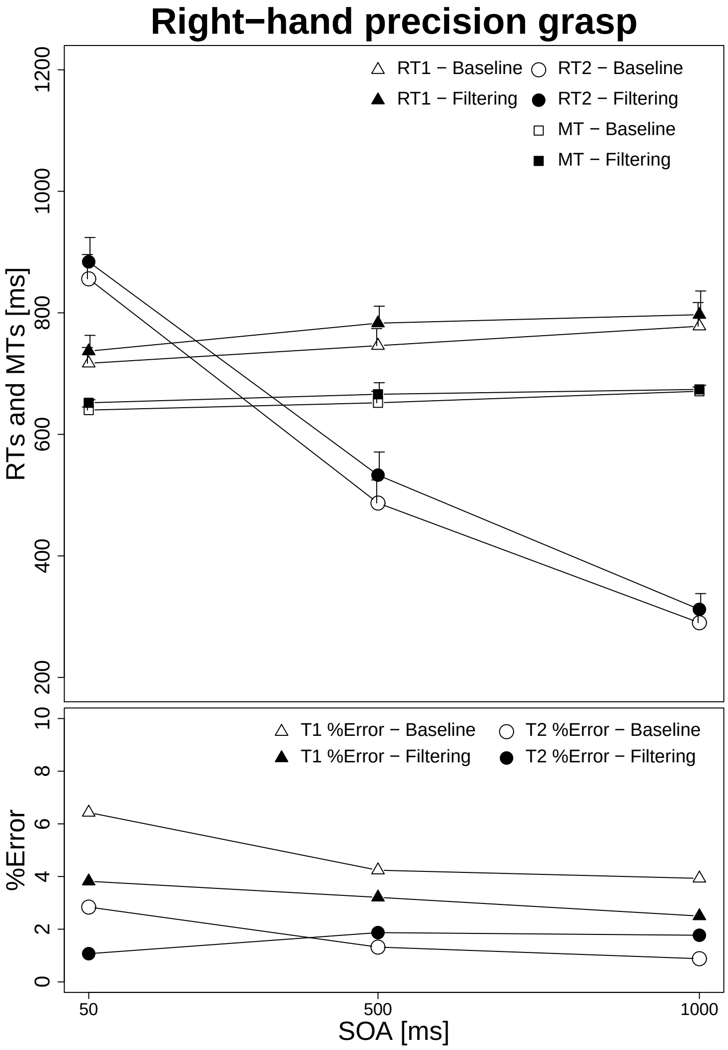


Figure 5.5: Mean response times (RT) and movement times (MT) in milliseconds, and mean error percentages (%Error) from Experiment 3 as a function of stimulus onset asynchrony (SOA) and condition. Error bars are 95% within-subject confidence intervals according to Loftus and Masson (1994), calculated across the factor condition.

5.3.3 Discussion

In Experiment 3, participants took part in a PRP experiment with a grasping task as T_2. Critically, and different to Experiments 1 and 2, R_1 were vocal utterances instead of manual key presses. This was done to ensure minimal effects of bimanual interference (e.g., Heuer, 1995) and/or competition for a specific resource pool (e.g., Navon, 1984; Wickens, 1980, 1984) related to response modality overlap. This new design also resulted in standard (stimulus–response) pairings (Hazeltine et al., 2006) that have been shown to favor parallel processing without considerable dual-task costs (at least after extensive practice)[2].

Despite this modification, the central and most critical finding remained stable: RTs in the grasping task were longer with shorter SOAs than with longer SOAs – the PRP effect. Similar to Experiment 1, and again not compatible with either central bottleneck models (Pashler, 1994) or capacity sharing models (Tombu & Jolicoeur, 2003), is the increase of RT_1 with an increasing SOA. However, since at the same time error rates decreased, this fact might again reflect a speed–accuracy trade–off in T_1. The reason for the slight, but significant, increase in MTs is unclear to me, and likely represents a random finding.

5.4 Integrative discussion of Experiments 1-3

In the following sections I will provide a conjoint discussion of Experiments 1-3. I will first focus on central capacity requirements for grasping, followed by assessing Garner-Interference as observed in Experiment 1.

5.4.1 Dorsal processing requires central capacity

According to the Action-Perception Model (Goodale & Milner, 1992; Milner & Goodale, 2006) as sketched in Chapter 2.1, the same visual input is processed by two different cortical systems for different purposes, a ventral 'vision for perception' stream and a dorsal 'vision for action' stream. Among other differences, it has been suggested that both streams differ in their consciousness and need for central capacity. In particular, dorsal processing has been described as effortless, fast, and automatic, thus not needing central processing

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[2] Admittedly, planning processes for vocal utterances can potentially interfere with the planning of the hand movement. Still, the amount of overlap is conceivably smaller in the case of one vocal and one manual response compared to two manual responses. Also, the combination of an auditory-vocal and a visual-manual task is a common feature of many though not all PRP studies in the literature as an attempt to minimize input and output interference. It has been shown to be the optimal pairing to reduce these types of interference in non-PRP studies (Shaffer, 1975).

capacity (e.g., Jeannerod & Jacob, 2005; Liu et al., 2008; Norman, 2002). A recent study (Kunde et al., 2007) using the PRP paradigm seriously questioned this assertion by demonstrating that a dorsal grasping task exhibits a PRP effect of the same size as a ventral perceptual judgment task (both tasks were modeled after Ganel & Goodale, 2003). Apparently, dorsal processing required some central capacity, and this contrasts with the Action-Perception Model. Unfortunately, the reported PRP effect could have been due to (at least) two alternative interpretations. First, the participants strategically withheld the grasping initiation to comply with the instruction to respond in stimulus order, i.e., first respond to T_1, then to T_2. Secondly, since both tasks required a manual response, the observed interference could be attributed to an overlap in response modalities (Heuer, 1995; Navon, 1984; Wickens, 1980, 1984).

The primary goal of Experiments 1-3 was to rule out these alternative accounts. To this end, I conducted three PRP experiments in which T_1 was always a binary tone classification. In Experiment 1, I used a modified instruction allowing a freely chosen response order (as was done by Ruthruff et al., 1995), and in Experiment 2, I took another step towards inducing parallel processing of both tasks and abandoning a prefered response order by introducing negative SOAs (Pashler et al., 1993) and a higher likelihood of short SOAs (Miller et al., 2009). Finally, in Experiment 3, I replaced the manual R_1 with a vocal response. This minimized the overlap in response modalities and such a standard pairing favors parallel processing (Hazeltine et al., 2006). The main outcome of all three experiments can be summarized quickly: I successfully replicated the PRP effect in the grasping task, thus re-assuring the idea that – from the viewpoint of the PRP paradigm – dorsal processing calls for central resources and cannot be construed as automatic. Corroborating this conclusion, considerable dual-task interference has also been observed in a study by Singhal et al. (2007). In contrast, Liu et al. (2008) and Lee and Hsieh (2009) came to a different conclusion. In their experiments, an RSVP task was combined with a pointing movement to a second peripheral target (either a to–be–identified letter or a simple disc) following the first target after a variable delay (their Experiment 1). The main result was that (successful) identification of the first target interfered with the initiation time of the pointing movement, but not with the movement time. Referring to Goodale and Milner (2004a), the authors predicted these results, since "action planning and action execution are controlled by the ventral and dorsal streams, respectively" (Liu et al., 2008, p. 710). Although this is true, the term "planning" is used in a vague and loose way here and does not match the use within the framework of the Action-Perception Model. Planning in a broad sense such as "deciding upon one course of action rather than another" is indeed attributed to the ventral stream (Goodale, 2008, p. 904). In contrast, planning in the sense of programming the initial movement parameters is nevertheless dependent on dorsal processing (Goodale & Milner, 2004a, p. 38). Conceivably, decisions like action–selection, the goal of the action, grip type (see also van Doorn, Kamp & Savelsbergh, 2007) and so on are inherent in the instructions and thus have already been established in the studies by Liu et al. (2008) and Lee and Hsieh (2009). What is left is the final programming of the movement, and this is – according to Goodale and Milner (2004a) – done by the dorsal stream. As such, the initiation time measures dorsal rather than ventral processing and the results are well in line with the conclusions I have based on my Experiments 1-3. That MTs were largely unaffected by the SOA manipulation in these experiments indicates that all relevant programming by the dorsal stream has been finished before the movement itself is initiated.

A slightly different view on planning and controlling was proposed by Glover and Dixon (Glover, 2002, 2004; Glover & Dixon, 2001, 2002). In their planning-control model, early phases even after movement initiation should be under ventral control, and only later control phases are subject to the dorsal stream. The abovementioned argument that the RT interval measures ventral functioning makes more sense in the light of the planning-control model. However, the main empirical arguments for this model were dynamic illusory effects, i.e., large initial illusory effects that diminish as a grasp progresses. Such dynamic illusory effects were subsequently difficult to replicate, and were attributed to statistical and methodological artifacts (e.g. Franz, 2003b; Franz, Scharnowski & Gegenfurtner, 2005), rendering the main evidence for this model rather weak and little convincing, and I thus refrain from going into more details here,

5.4.2 Garner-Interference as an indicator for ventral processing

A second goal of Experiment 1 was to replicate the occurence of Garner-Interference with a ventral task within the PRP paradigm, thus to replicate the results of Kunde et al. (2007). According to Ganel and Goodale (2003) the occurence of Garner-Interference indicates a ventral processing mode, whereas its absence indicates a dorsal processing mode. Despite the minor qualification mentioned in the discussion of Experiment 1, I am convinced that Experiment 1 was still successful in this regard. In sum, there exist by now three independent observations of this effect: my Experiment 1 plus the studies by Ganel and Goodale (2003) and Kunde et al. (2007). Against this background I feel confident using the absence and presence of Garner-Interference as a reasonable behavioral indicator for an underlying dorsal or ventral processing mode, respectively.

Noteworthy, Garner-Interference (in the perceptual judgment task of Experiment 1) combined additively with the SOA, exactly as previously observed by Kunde et al. (2007). According to the logic outlined in Chapter 3, this suggests that Garner-Interference is resolved only at a central (or even post-central) processing stage (see also Pashler, 1994). This is surprising since Ganel and Goodale (2003, p.664) suggested that for holistic processing "a given dimension cannot be *perceptually* isolated from the other dimensions of the object" [emphasis by me]. It might thus be that, although somewhat counterintuitive, resolving Garner-Interference (and thus the isolation of object dimensions) is an example of perceptual phenomena requiring central processing resources (see Pashler & Johnston, 1998). I will come back to this issue and discuss theoretical implications of this finding in Section 7.3.

5.5 Summary and outlook for Experiments 4-7

To summarize, the results from Experiments 1-3 support the conclusion that dorsal processing is not automatic but rather requires central capacity and interferes with concurrent tasks. For the PRP and attention researcher, this might come to some disappointment, since dorsal processing was indeed a likely candidate for an exception from the robust PRP effect. Additionally, Garner-Interference was replicated with the ventral perceptual judgment task in Experiment 1. Supported by two other and independent observations (Ganel & Goodale, 2003; Kunde et al., 2007), I feel confident to use Garner-Interference as a behavioral indicator for ventral processing in the subsequent Experiments 4-7. The main purpose of these experiments was to test whether left-handed and/or unskilled grasping is indeed controlled ventrally, as was recently claimed (Gonzalez et al., 2006, 2008).

6 Experiments 4-7: Which actions escape dorsal processing?

From its very beginning the Action-Perception Model assumed that several classes of movements rely on perceptual information provided by the ventral stream instead of being handled by the dorsal stream. In particular, this was suggested for movements without direct visual input or those not directed at a real object, such as pantomiming or delayed movements (Goodale et al., 1994, 2004). Recently, for left-handed[1] and unskilled grasping reliance on ventral perceptual information has been suggested, too (Gonzalez et al., 2006, 2008). In some original words (italics added by me):

> ”Even though practice might make *movements with the left hand* faster and more efficient, the visual control of these movements *cannot escape the relational metrics that characterize visual perception. Only movements with the right hand [...] make use of real world metrics.*” (Gonzalez et al., 2008, p. 630) or
>
> ”Recent experiments have shown that for actions to escape the effects of such illusions, however, they must be *highly practised actions, preferably with the right hand*, and must be directed in real time at visible targets.” (Goodale, 2008, p. 891)

In comparison with pantomiming or delayed-grasping, left-handed and unskilled grasping is of particular interest, since they (1) are directed at objects and (2) can be performed under full vision of this target-object.

However, thus far such claims were exclusively based on visual illusory effects on left-handed and unskilled grasping. Earlier, in Section 2.3, I have argued that the (non-

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[1] It is tempting to add ”in right-handers” here, but this would not correctly reflect the theory. Gonzalez et al. (2006) indeed claimed that even in left-handers only right-handed movements are controlled by the dorsal stream. This strong claim has been criticized heavily (Derakhshan, 2006), and in a reply Gonzalez, Goodale and Ganel (2006) admitted that this was only a ”tentative idea”. In the present work I only consider the more cautious assumption that left-handed movements in right-handers are controlled by the ventral stream.

)existence of effects of visual illusions on action is still quite controversial (Franz & Gegenfurtner, 2008; Goodale, 2008). In addition, results from other studies are not unambigious. On the one hand, it was shown that left-handed reaching is more sensitive to irrelevant placeholders, thus the visual context, than right-handed reaching is (Adam, Müskens, Hoonhorst, Pratt & Fischer, 2010). On the other hand, Radoeva, Cohen, Corballis, Lukovits and Koleva (2005) found no difference in illusion effects between left- and right-handed grasping and the Brentano illusion also affects both hands to the same extent (de Grave, Brenner & Smeets, 2009).

In light of these ambigious results and the controversial discussion around the thus far used indicator (the effect of visual illusions on perception and action) I consider it necessary to investigate left-handed and unskilled grasping in more detail, but with a different approach. In particular, the following Experiments 4-7 will make use of a different indicator than visual illusions, namely Garner-Interference (see Section 2.6 and Ganel & Goodale, 2003). If left-handed or unskilled grasping indeed relies more on perceptual information (Gonzalez et al., 2006, 2008) provided by the ventral stream (as opposed to the dorsal stream, which applies for right-hand precision grasping) these movements should produce Garner-Interference. Experiment 4 adresses this point for left-handed grasping, Experiments 5-7 for unskilled grasping.

Similar to Experiments 1-3, the following experiments (except for Experiment 6) are settled within the PRP paradigm for two reasons. First, as shown in Experiments 1-3 a (dorsal) right-hand precision grasp is subject to the PRP effect, i.e., entails a central processing stage (see also Kunde et al., 2007). For better comparability with these experiments and to generalize this finding to other classes of grasping movements, I applied the PRP paradigm here, too. Secondly, so far Garner-Interference in perceptual judgment tasks combined additively with the dual-task factor SOA (see Experiment 1 and Kunde et al., 2007). According to the PRP logic and the central bottleneck model (Chapter 3) this suggests the implication of a central stage in resolving Garner-Interference. At first glance, this appears somewhat counterintuitive since Garner-Interference can be seen as a perceptual phenomenon (which should result in an underadditive combination with SOA; Pashler (1994), Pashler and Johnston (1998), and Chapter 3). Given that the occurence of Garner-Interference in left-handed and unskilled grasping would be predicted, it is of interest whether it again produces an additive interaction with SOA.

6.1 Experiment 4

In this experiment, I tested whether left-handed (precision) grasping is under ventral control, as suggested by Gonzalez et al. (2006). In contrast to this study, I used Garner-Interference (instead of visual illusory effects) as indicating an underlying ventral mode of processing.

6.1.1 Method

Participants

Sixteen new undergraduate students 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 checked informally by the experimenter when participants were to note their date of birth on a sheet of paper).

Design, apparatus, stimuli, procedure, and data treatment and analyses

This experiment resembles the grasping condition of Experiment 1 with three changes. First, all participants took part in only one session with grasping as T_2. Secondly, participants were to use a left-handed precision grip and responses to T_1 were given with the right hand. Thirdly, instructions prioritized T_1 performance.

6.1.2 Results

RT and MT analyses

Mean RTs and MTs are visualized in Figure 6.1 (for details see Table B.4). Mean RT_1 was, overall, slightly longer in the filtering condition compared to the baseline condition and increased with an increasing SOA. The latter finding was confirmed by a significant main effect of SOA; $F(2, 30) = 9.28$, $p < .01$, $\eta_P^2 = .38$, $\epsilon = .55$. No other effect was significant; condition: $F(1, 15) = 0.22$, $p = .64$, $\eta_P^2 = .02$; SOA × condition: $F(2, 30) = 1.39$, $p = .26$, $\eta_P^2 = .09$, $\epsilon = .64$.

Mean RT_2 showed, like in Experiments 1 and 3, a large decrease with increasing SOA, supported by a significant effect of SOA; $F(2, 30) = 756.76$, $p < .01$, $\eta_P^2 = .98$, $\epsilon = .71$. Of most importance to the present purposes, however, the difference between conditions was not reliable; $F(1, 15) = 0.02$, $p = .89$, $\eta_P^2 < .01$; nor was the interaction; $F(2, 30) = 0.28$,

$p = .69$, $\eta_P^2 = .02$, $\epsilon = 71$. Mean MTs varied between 642 and 667ms, no effect was significant (all p's $> .08$).

Error analyses

Mean percentages of errors are visualized in Figure 6.1 (for details see Table B.4), and there was one significant effect. Similar to earlier experiments, mean error percentages in T_1 tended to decrease with an increasing SOA; $F(2, 30) = 5.66$, $p < .01$, $\eta_P^2 = .27$.

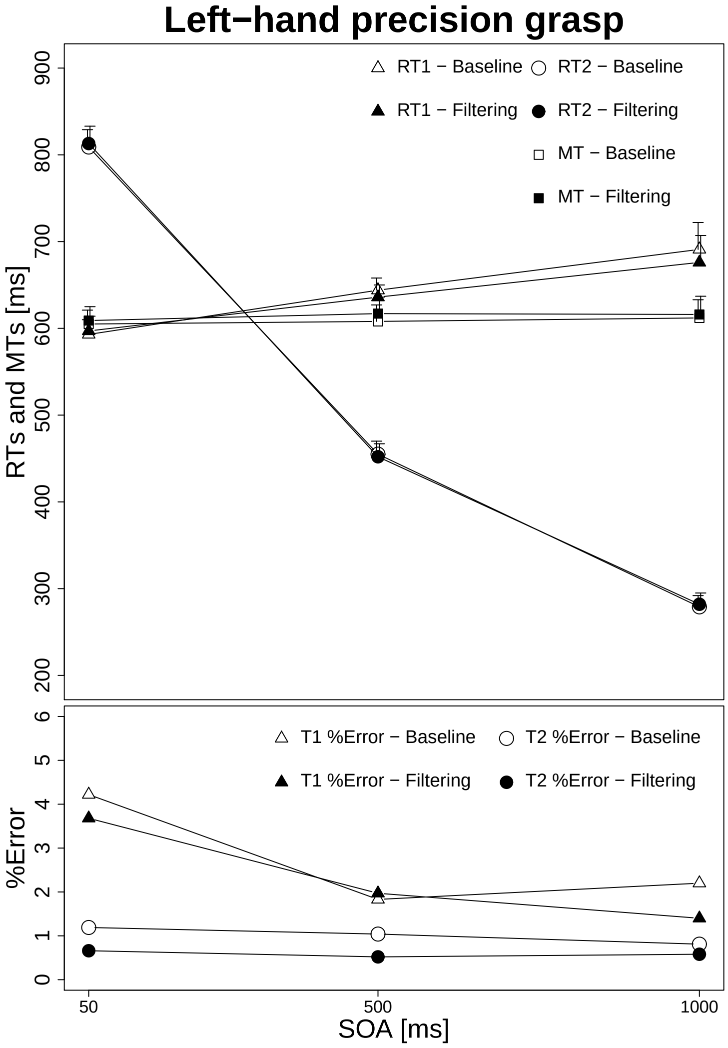


Figure 6.1: Mean response times (RT) and movement times (MT) in milliseconds, and mean error percentages (%Error) from Experiment 4 as a function of stimulus onset asynchrony (SOA) and condition. Error bars are 95% within-subject confidence intervals according to Loftus and Masson (1994), calculated across the factor condition.

6.1.3 Discussion

Experiment 4 was run to assess whether left-handed grasping (in right-handers) relies on ventral instead of dorsal processing (Gonzalez et al., 2006). If this would be true, Garner-Interference (i.e., an RT difference between baseline and filtering conditions) should emerge. In addition, I tested for a PRP effect. First, the data show the typical pattern observed in a PRP experiment. RT_1 was largely unaffected by any manipulation, but nevertheless showed a small increase with an increasing SOA. (Similar to the previous experiments, I attribute this to a speed–accuracy trade–off). In contrast, RT_2 decreased about 500ms with an increasing SOA - the PRP effect. The previous reports of non-automatic dorsal processing of grasping (my Experiments 1-3 and Kunde 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: there was no hint for Garner-Interference with left-handed grasping, indicating that the involved planning mechanisms were able to efficiently ignore the task-irrelevant variation of stimulus length. Crucially, this ability has been ascribed to the dorsal stream (Ganel & Goodale, 2003). Thus, using Garner-Interference as the indicator, leads to a conclusion contrasting the one drawn by Gonzalez et al. (2006) on the basis of illusory effects on left-handed grasping. Rather, I need to conclude that there is no difference between left- and right-handed precision grasping (at least in right-handers) in terms of the underlying processing mode.

6.2 Experiment 5

According to the non-occurence of Garner-Interference in Experiment 4, left-handed grasping relies on the dorsal stream. A second candidate action for ventral control has been identified with unskilled grasping (Gonzalez et al., 2008). Experiment 5 is essentially the same as Experiment 4, but, as in the Gonzalez et al. (2008) study, participants used an 'awkward grip' with their thumb and ring-finger. Again, the main purpose was to test whether Garner-Interference would occur indicating a ventral mode of processing for this kind of action.

6.2.1 Method

Participants

Sixteen new undergraduates from Dortmund University of Technology (3 male, mean age = 22;4 years) participated in return of course credit. All participants were right-handed (by self-report).

Design, apparatus, stimuli, procedure, and data treatment and analyses

This experiment was very similar to Experiments 1 and 4. Participants used an (unskilled) awkward grip between their thumb and ring-finger of their right hand, similar to the study by Gonzalez et al. (2008) (see Figure 6.2). As a consequence, R_1 was given with the left hand. 3.3% and 3.3% of the trials were excluded as outliers in T_1 and T_2, respectively.

Figure 6.2: Illustration of the (unskilled) awkward grip used in Experiments 5 and 6 (see also Gonzalez et al., 2008).

6.2.2 Results

RT and MT analyses

Mean RTs and MTs are visualized in Figure 6.3 and summarized in Table B.5, and overall the results left the same impression as those from Experiment 4. Mean RT_1 was slightly longer in the filtering condition compared to the baseline condition and increased with an increasing SOA. The latter finding was confirmed by a significant main effect of SOA; $F(2,30) = 10.11$, $p < .01$, $\eta_P^2 = .40$, $\epsilon = .70$. No other effect was significant; condition: $F(1,15) = 3.65$, $p = .08$, $\eta_P^2 = .20$; SOA × condition: $F(2,30) = 2.28$, $p = .12$, $\eta_P^2 = .13$.

Mean RT_2 exhibited the typical PRP effect supported by a significant effect of SOA; $F(2,30) = 157.29$, $p < .01$, $\eta_P^2 = .91$, $\epsilon = .61$. In contrast, and most important, again no difference between conditions was found; $F(1,15) = 0.02$, $p = .89$, $\eta_P^2 < .01$. The interaction was not significant, too; $F(2,30) = 0.06$, $p = .94$, $\eta_P^2 < .01$. Mean MTs varied from 605ms to 617ms, and no effect was significant (all p's$> .28$).

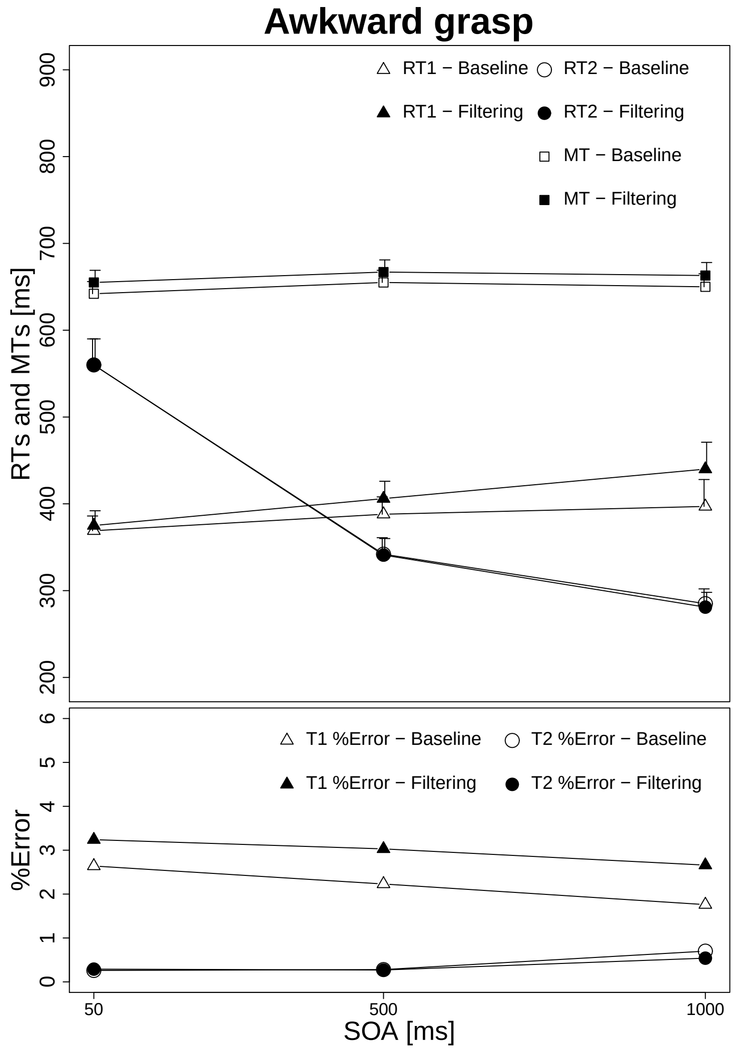


Figure 6.3: Mean response times (RT) and movement times (MT) in milliseconds, and mean error percentages (%Error) from Experiment 5 as a function of stimulus onset asynchrony (SOA) and condition. Error bars are 95% within-subject confidence intervals according to Loftus and Masson (1994), calculated across the factor condition.

Error analyses

Mean percentages of errors are visualized in Figure 6.3 (for details see Table B.5). No effect reached significance.

6.2.3 Discussion

In Experiment 5 I investigated awkward grasping (see Figure 6.2). This grip type was previously used as an example for an unskilled action by Gonzalez et al. (2008). The results are almost identical to what I observed in Experiment 4. 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 (Ganel & Goodale, 2003). This interpretation – again – contrasts the one advanced by Gonzalez et al. (2008) based on an effect of visual illusions on awkward grasping.

6.3 Experiment 6

Experiments 4 and 5 were PRP experiments, where the particular grasping task was implemented as T_2. The reason for this was that I expected Garner-Interference, as the used grasping types were suggested relying on ventral information (Gonzalez et al., 2006, 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, I ran Experiment 6 as a single-task experiment where participants used again the awkward grip (see Figure 6.2).

6.3.1 Method

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).

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 5 to grasp the stimulus blocks (see Figure 6.2). Details on the baseline and filtering conditions can be found in the method section of Experiment 1. Every trial began with a short warning click, and after 800 or 1200ms (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.

6.3.2 Results and discussion

Mean RTs, MTs, and mean error percentages are summarized in Table 6.1. Condition had no significant effect on either dependent measure; RTs: $F(1,15) = 0.35$, $p = .56$, $\eta_P^2 = .02$; MTs: $F(1,15) = 0.24$, $p = .63$, $\eta_P^2 = .02$; mean percentage of errors: $F(1,15) = 0.78$, $p = .79$, $\eta_P^2 = .01$. This result suggests that also under single-task conditions no Garner-Interference was observed for awkward grasping, pointing to a dorsal mode of processing (Ganel & Goodale, 2003). As such, the claims made from Experiments 4 and 5 are further strenghtened.

Table 6.1: Mean response times (RT) and movement times (MT) in milliseconds, and mean error percentages (%Error) from Experiment 6 as a function of condition.

	Condition	
	Baseline	Filtering
RTs	316	311
MTs	634	639
%Error	1.56	1.48

6.4 Experiment 7

Experiments 4-6 left a rather disappointing picture. Neither left-handed grasping (Experiment 4) nor unskilled (awkward) grasping (Experiments 5 and 6) showed any signs of Garner-Interference. This outcome is actually predicted if one assumes that the involved planning mechanisms and processes were able to ignore the task-irrelevant variation of the stimuli' length, but this ability has been ascribed to dorsal processing by Ganel and

Goodale (2003) and I thus must conclude that both left-handed and awkward grasping were controlled by this very mode. Taking this interpretation for serious, my results (based on Garner-Interference as the indicator) show exactly the opposite than those reported by Gonzalez et al. (2006, 2008), who used the effect of visual illusions on grasping as the indicator for a ventral stream's implication.

Before discussing the implications of these results I like to direct the attention to three issues. First, my interpretations so far are based on three null-findings, what immediately raises the question of whether I had employed enough statistical power. I suspect this an unlikely problem to my Experiments (actually, the mean RT_2 differences between baseline and filtering blocks were very small), but concur that a higher powered experiment would strengthen my interpretations. A second and related issue is that I have thus far not included any control condition to test whether Garner-Interference can be observed within the same participants. If the same participants would produce Garner-Interference in, e.g., the perceptual judgment task (used in Experiment 1), but at the same time not in a grasping task under investigation here, this would be compelling evidence for my 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 was thus controlled exactly as a normal, right-handed, precision grip. Hence the use of a different unskilled grasping action appears desirable.

In Experiment 7 I addressed these three points. To enlarge the power of the experiment I used $n = 32$ (instead of $n = 16$) 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 4-6 I expected to replicate the dual-task characteristics. More importantly, I expected the occurrence of Garner-Interference in the perceptual task, but not in the tool grasping task.

6.4.1 Method

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).

Design, apparatus, stimuli, procedure, and data treatment and analyses

Experiment 7 resembles Experiment 1 with few exceptions. First, instead of using a precision grip, participants were to grasp the stimulus blocks using pliers (see Figure 6.4). At the beginning of each trial they depressed the home button with the tip of these pliers. Secondly, instructions prioritized T_1 over T_2. Data analyses were mostly as introduced for Experiment 1, but the factor 'task' (tool grasping *vs.* perceptual judgment) was introduced as a third repeated measure.

With tool grasping as T_2, 3.7% and 4.0% of the trials in T_1 and T_2 were excluded as outliers; the corresponding values for perceptual judgment as T_2 are 3.3% and 3.0%

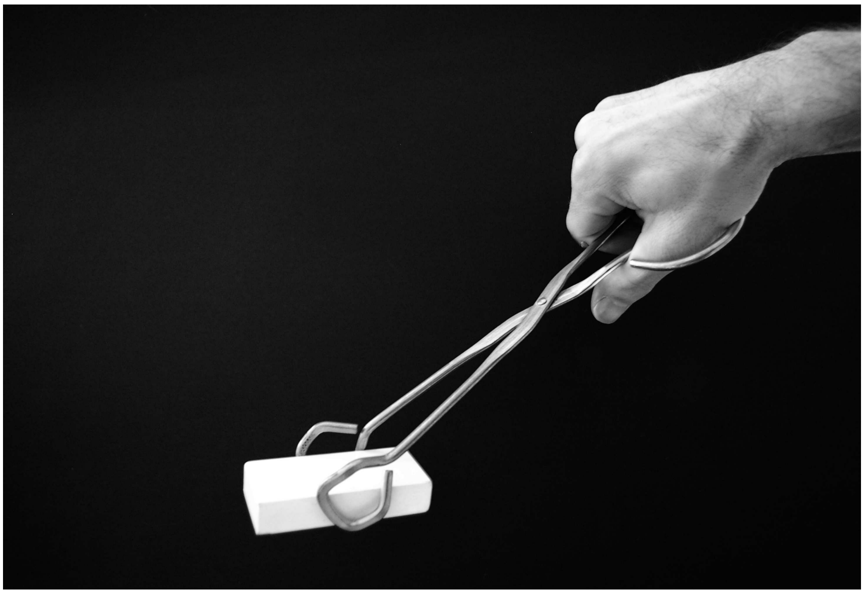


Figure 6.4: Illustration of the tool grasping task used in Experiment 7.

6.4.2 Results

RT and MT analyses

Mean RTs and MTs are visualized in Figure 6.5 (for details see Table B.6). Mean RT_1 was longer with perceptual judgment than with tool grasping as T_2; $F(1,31) = 27.44$, $p < .01$, $\eta_P^2 = .47$. There was a main effect of SOA; $F(2,62) = 4.97$, $p = .03$, $\eta_P^2 = .14$, $\epsilon = .57$, but this main effect was modified by a significant interaction of SOA × task; $F(2,62) = 10.46$, $p < .01$, $\eta_P^2 = .25$, $\epsilon = .61$: whereas mean RT_1 was rather unaffected by SOA with perceptual judgment as T_2, it increased with an increasing SOA with tool grasping as T_2.

No other effects were significant; condition: $F(1,31) = 3.78$, $p = .06$, $\eta^2_P = .11$; task × condition: $F(1,31) = 0.02$, $p = .90$, $\eta^2_P < .01$; SOA × condition: $F(2,62) = 0.18$, $p = .84$, $\eta^2_P = .01$; SOA × condition × task: $F(2,62) = 0.17$, $p = .84$, $\eta^2_P = .01$

Mean RT_2 was longer with perceptual judgment than with tool grasping as T_2; $F(1,31) = 138.92$, $p < .01$, $\eta^2_P = .82$; and showed a decrease with an increasing SOA - the PRP effect; $F(2,62) = 320.77$, $p < .01$, $\eta^2_P = .91$, $\epsilon = .61$. This decrease was roughly the same for both T_2 types, yielding a non-significant interaction SOA × task; $F(2,62) = 2.03$, $p = .16$, $\eta^2_P = .06$, $\epsilon = .63$. Of most importance for the present purposes was the significant main effect of condition with longer RTs in filtering than in baseline blocks (i.e., Garner-Interference); $F(1,31) = 6.82$, $p = .01$, $\eta^2_P = .18$. However, this main effect was further modulated by the interaction condition × task; $F(1,31) = 7.94$, $p = .01$, $\eta^2_P = .20$: the size of Garner-Interference was about 100ms in the perceptual judgment task, at the same time Garner-Interference was nearly absent in the tool grasping task. No other effect was significant; SOA × condition: $F(2,62) = 1.12$, $p = .34$, $\eta^2_P = .03$; SOA × condition × task: $F(2,62) = 1.29$, $p = .28$, $\eta^2_P = .04$

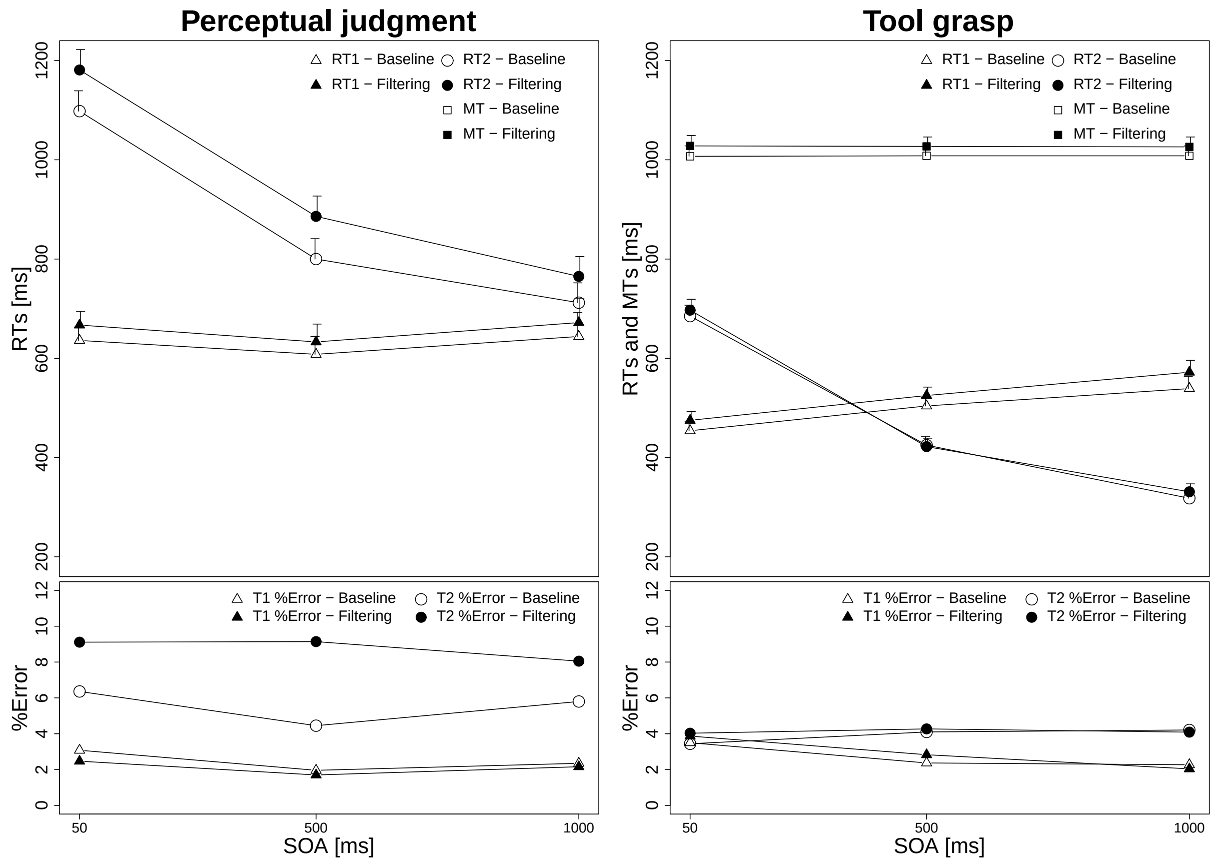
Mean MTs were higher than those observed in the previous experiments, and varied between 1007ms and 1028ms, but no effect reached significance (all p's$> .15$).

Error analyses

Mean percentages of errors are visualized in Figure 6.5 (for details see Table B.7). There were several significant effects. Mean error percentages in T_1 decreased with an increasing SOA (numerically more obvious with tool grasping as T_2); $F(2,62) = 5.82$, $p = .01$, $\eta^2_P = .12$. Mean error percentages in T_2 were higher for perceptual judgment than for tool grasping; $F(2,30) = 12.19$, $p < .01$, $\eta^2_P = .28$; and were also higher in filtering blocks than in baseline blocks; $F(1,31) = 12.28$, $p < .01$, $\eta^2_P = .28$. This main effect, however, was modulated by the interaction task × condition; $F(1,31) = 5.96$, $p = .02$, $\eta^2_P = .15$; indicating that the difference between filtering and baseline blocks was only evident in the perceptual judgment task. In other words: Garner-Interference was observed for mean error percentages, too. No other effect was significant.

6.4.3 Discussion

Experiments 4-6 have consistently shown that left-handed grasping and (unskilled) awkward grasping are not susceptible to Garner-Interference. According to the logic of Ganel



(a) (b)

Figure 6.5: Mean response times (RT) and movement times (MT) in milliseconds, and mean error percentages (%Error) from Experiment 7 as a function of stimulus onset asynchrony (SOA) and condition. (a) Perceptual judgment as T_2; (b) Grasping as T_2. Error bars are 95% within-subject confidence intervals according to Loftus and Masson (1994), calculated across the factor condition.

and Goodale (2003), this suggests a dorsal processing mode and contradicts recent proposals that these actions escape dorsal processing and are under ventral control (Gonzalez et al., 2006, 2008). In Experiment 7 I 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 T_2 in a PRP experiment, and in addition the participants were tested in a second session where T_2 was a perceptual judgment task. With this, presumably typical ventral, task Garner-Interference has repeatedly been shown (my Experiment 1; Ganel & Goodale, 2003; Kunde et al., 2007) and it thus served as a control condition in Experiment 7.

The results are summarized quickly, as they are very similar to those reported from Experiments 4 and 5. First, for both tasks (the tool grasping and the perceptual judgment task) I observed the typical dual-task behavior and both tasks appear to recruit a central stage of processing. Secondly, large Garner-Interference was found for the perceptual judgment task. This Garner-Interference combined additively with SOA as it did in Experiment 1 and in Kunde et al. (2007). Thirdly, and most important, despite this and doubling the sample size, the same participants showed no Garner-Interference in the tool grasping task. This result corroborates the conclusions made from Experiments 4-6 and reinforces the claim that neither left-handed nor unskilled grasping movements are controlled by a different processing stream than normal, right-handed grasping.

6.5 Integrative discussion of Experiments 4-7

6.5.1 No ventral contributions to left-handed and unskilled grasping

The main purpose of Experiments 4-7 was to test whether left-handed and/or unskilled grasping relies on perceptual information from the ventral stream, instead of being controlled by the dorsal stream (Gonzalez et al., 2006, 2008). These claims were based on effects of visual illusions on these grasping types. In contrast, I used Garner-Interference as the behavioral indicator of the underlying processing mode (Ganel & Goodale, 2003). I ran three dual-task PRP experiments plus one single-task experiment where different grasping tasks were implemented: in Experiment 4 the participants used a left-handed precision grip, in Experiments 5 and 6 they used an awkward grip with their right hand (see Figure 6.2), and in Experiment 7 they used pliers handled with their right hand (see Figure 6.4) to grasp small wooden blocks. The main results can be summarized quickly since they all converge in the same conclusion: never did I find Garner-Interference for any type of grasping. Following the reasoning of Ganel and Goodale (2003), I need to conclude that they all were mediated by the dorsal stream instead of relying on perceptual information provided by the ventral stream (or at least: by the same mechanisms guiding right-handed precision grasping). Obviously this contrasts with earlier suggestions (Gonzalez et al., 2006, 2008) and highlights the importance of independent evidence and the use of various methods, in the best case yielding converging evidence. In light of the controversial debate around the different illusory effects on action and perception, the present results are – at least at first glance – clear-cut: there is no need for distinguishing two classes of visually guided actions, one mediated 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.

Garner-Interference was observed for the perceptual judgment task in Experiment 7. Again, as in Experiment 1 and in Kunde et al. (2007), Garner-Interference combined additively with SOA suggesting - according to the central bottleneck model and the PRP logic (e.g., Pashler, 1994; Pashler & Johnston, 1998) - an involvement of central mechanisms here, although intuitively Garner-Interference comes across as a perceptual phenomenon. I will come back to this issue in Section 7.3.

6.5.2 The dual-task behavior of left-handed and unskilled grasping

The results allow also concluding that unskilled and left-handed grasping is subject to massive dual-task interference, by demonstrating a PRP effect in Experiments 4, 5, and 7. This is less surprising since even right-handed precision grasping is subject to dual-task interference (see Experiments 1-3, and Kunde et al., 2007). A (cautious) comparison across experiments will be provided in Section 7.1.2.

6.6 Summary

In sum, the results from Experiments 4-7 suggest that left-handed and unskilled grasping movements are controlled by similar mechanisms as skilled right-handed precision grasping is. Thus, there is no need to distinguish several classes of visually guided (grasping) actions, which are controlled by different processing streams. Notably, this conclusion contradicts those made by Gonzalez et al. (2006, 2008) based on illusory effects on such grasps. There are implications for applied research regarding which characteristics of 'natural' actions generalize to transformed and other artificial movements (see, e.g., Kunde, Müsseler & Heuer, 2007), but for a further discussion, please see Section 7.4.

7 General Discussion

The General Discussion is split into several sections. To recap, I will start by briefly summarizing the purposes of this study plus the most relevant results, supplemented with a comparison across experiments. Implications of these results for PRP/dual-task research and the Action-Perception Model will subsequently be discussed followed by some limiting comments and an outlook for future research.

7.1 Summary of the present study

7.1.1 The theoretical purposes...

The Action-Perception Model (e.g., Goodale & Milner, 1992; Milner & Goodale, 1995, 2006) states that the ventral and the dorsal stream (Ungerleider & Mishkin, 1982) process – more or less – the same visual input but for different purposes: the ventral stream creates the conscious percept of our visual surroundings and makes recognition possible through an interaction with memory (= 'vision for perception'). In contrast, the dorsal stream should be implicated in the programming and control of visually guided actions, in the present study the investigated action was grasping (= 'vision for action'). Several authors have suggested that processing in the dorsal stream is automatic and effortless (e.g., Goodale & Milner, 2004b; Jeannerod & Jacob, 2005; Liu et al., 2008; Norman, 2002), but empirical results are ambigious. Recently, a PRP effect of roughly the same size was reported for grasping and a perceptual judgment task (Kunde et al., 2007)[1]: at first glance convincingly contrasting the 'dorsal automaticity claim', but yet open to two alternative explanations. Experiments 1-3 were run to replicate the PRP effect for grasping, while carefully testing these alternatives. A side aspect of Experiment 1 was to replicate Garner-Interference (see Section 2.6 or Ganel & Goodale, 2003) for a perceptual judgment task that is assumed as being under ventral control.

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[1] I will briefly discuss the validity of such comparisons in a later section.

This latter aspect became important in Experiments 4-7. In addition to pantomiming (Goodale et al., 1994) and delayed grasping (Goodale et al., 2004) recently also left-handed and unskilled grasping have been suggested to rely on perceptual information from the ventral stream. This claim was based on finding visual illusory effects on left-handed and unskilled grasping (Gonzalez et al., 2006, 2008) – an indicator that is discussed quite controversial (see Section 2.3 and for recent reviews Franz and Gegenfurtner (2008) and Goodale (2008)). Results from other studies are also not clear-cut (Adam et al., 2010; de Grave et al., 2009; Radoeva et al., 2005), and against this background the search for other indicators is deemed necessary. One such indicator is Garner-Interference, as was suggested by Ganel and Goodale (2003): the ventral stream's inability to ignore task-irrelevant stimulus dimensions yields longer *RT*s when such dimensions vary. Empirically, Garner-Interference was reported for a perceptual judgment task by Ganel and Goodale (2003) and – under dual-task conditions – by Kunde et al. (2007). My Experiment 1 replicated the latter study, and I felt confident using Garner-Interference to assess whether or not left-handed and/or unskilled grasping relies on ventral information in Experiments 4-7.

7.1.2 ...and the empirical results

In the following I briefly discuss the most relevant results from my experiments separately for the two major questions raised in Chapter 4 and summarized above. This will be followed by a brief comparison across the reported (PRP) experiments, as far as regarded helpful and theoretically interesting.

Central capacity requirements

In the present study the PRP effect was used to assess central capacity requirements of various grasping movements (right-handed and left-handed precision-grasping, (unskilled) awkward grasping, and (unskilled) tool grasping). To reiterate, the PRP effect is thought to arise if two tasks rely on a common (central) resource or both encompass a central processing stage, of which the cognitive system can only handle one at any time (see Section 3.2 for more details).

Across all my PRP experiments a PRP effect was clearly present, thus suggesting the implication of central resources or a central bottleneck processing stage in grasping, similar to the finding earlier reported by Kunde et al. (2007). Importantly, in my Experiments 1-3 this PRP effect was observed despite careful control of strategic response deferments and a lack of (input and) output modality overlap. Put differently: visually guided grasping cannot be construed as automatic and effortless as was claimed previously (Enns & Liu, 2009; Goodale & Milner, 2004b; Jeannerod & Jacob, 2005; Liu et al., 2008; Norman, 2002). Rather, grasping seems to interfere with other – even simple – tasks (see also Singhal et al., 2007).

Given these results: how can such a central resource best be described? Note that, in a sense, the notion of a (limited) processing resource does encompass the assumption of a processing stage that can only handle one process at any time (see, e.g., Navon & Miller, 2002). This is also reflected in the fact that the capacity sharing model of Tombu and Jolicoeur (2003) predicts the same as does the central bottleneck model (e.g., Pashler, 1994) when all capacity is allocated to T_1 first. The main distinction appears thus whether this resource can be allocated in a graded or only in an all-or-none fashion. Crucially, some instance of higher-order executive control needs to be theorized that is in charge to establish these graded resource allocations. Still, the exact nature of resources remains mostly unclear to date. Some researchers have likened it to a general-purpose pool of 'mental energy' or 'fuel' – such as attention – that can be directed (in varying proportions) to several tasks (e.g., Kahneman, 1973; Navon & Gopher, 1979), and that can even be augmented by putting more effort into the current tasks. Such graded resource theories have not remained uncriticized (see, e.g., Wickens, 1980) and it must be awaited which concept eventually becomes accepted. A detailed discussion of this theoretically highly important topic is, however, beyond the scope of the present work.

Action control modes

Following the logic of Ganel and Goodale (2003), tasks that are processed by the ventral stream should produce Garner-Interference, while its absence suggests a dorsal stream implication. First, Garner-Interference was present with a typical (ventral) perceptual judgment task (Experiments 1 and 7): judging the width of the stimulus blocks. Secondly, and as expected, for right-handed precision grasping no Garner-Interference was observed in either Experiment 1 or 3. Thirdly, however, even with left-handed and (unskilled) awkward or tool grasping, no Garner-Interference was observed (Experiments 4-7). As such, all here investigated grasping types share the ability to ignore task-irrelevant stimulus dimensions, what has been ascribed to the dorsal stream (Ganel & Goodale, 2003).

Note that this claim is based on null-findings, i.e., a non-significant effect of condition (baseline *vs.* filtering) on the dependent measures. This immediately raises the question of the analyses' statistical power and the corresponding probability of a type-II-error. Power analysis using G-Power (Faul, Erdfelder, Lang & Buchner, 2007) yields a necessary sample size of $n = 11$ to detect a large effect of Cohen's $f = .40 \Leftrightarrow \eta_P^2 = .1379$ (Cohen, 1988) with a power of $1 - \beta = .95$. Note that the true effect (calculated from the perceptual judgment task in Experiment 7) was $\eta_P^2 = .20 \Leftrightarrow f = .5$, thus even larger than the assumed large effect (For the power analysis I used $\alpha = .05$ and $\rho = .8$, the observed correlation between both conditions was $r = .83$.). In sum, the required sample size was met in all reported experiments, what puts retaining the null-hypothesis on a safer ground and supports the conclusions made.

Comparison across experiments

It is tempting to compare the PRP effects across the reported PRP experiments and to draw conclusions about the amount of dual-task interference from such comparisons. Such analyses are not uncommon (e.g., Bratzke, Rolke, Ulrich & Peters, 2007), yet they are not valid. Nevertheless, Figure 7.1 illustrates mean RT_1 and RT_2 (both only for the SOA=1000ms, i.e., without much task overlap), MT, and the mean PRP effect (calculated according to Equation 3.1) from the grasping tasks of Experiments 1, 3, 4, 5, and 7. With 'experiment' as a between-subject factor, an ANOVA on the mean PRP effect was significant; $F(4, 91) = 13.88$, $p < .01$, $\eta_P^2 = .38$. From Figure 7.1 one can infer that the PRP effect for awkward grasping (Experiment 5) was smaller than for left-handed grasping (Experiment 4). Does this mean that awkward grasping required less central capacity? Self-evident at first glance – but still wrong. As is shown in Appendix A the quantified PRP effect is a function of RT_1 (or at least of the pre-central and central stage of T_1), but importantly, not of the central stage of T_2. In other words: the size of the PRP effect does not allow any conclusions about the duration of T_2 central processing. Note that mean RT_1 (in Figure 7.1) closely follows the variation of the PRP effect (the corresponding ANOVA on RT_1 was also significant; $F(4, 91) = 7.19$, $p < .01$, $\eta_P^2 = .88$). It is thus reasonable to attribute any differences in the PRP effects to the corresponding RT_1 variation.

If one wants to draw inferences about (relative) lengths of central stages for different types of grasping, two conditions must be met: (1) grasping must be implemented as T_1 and (2) the duration of the pre-central stages (A_1 and A_2) must be assumed equal across

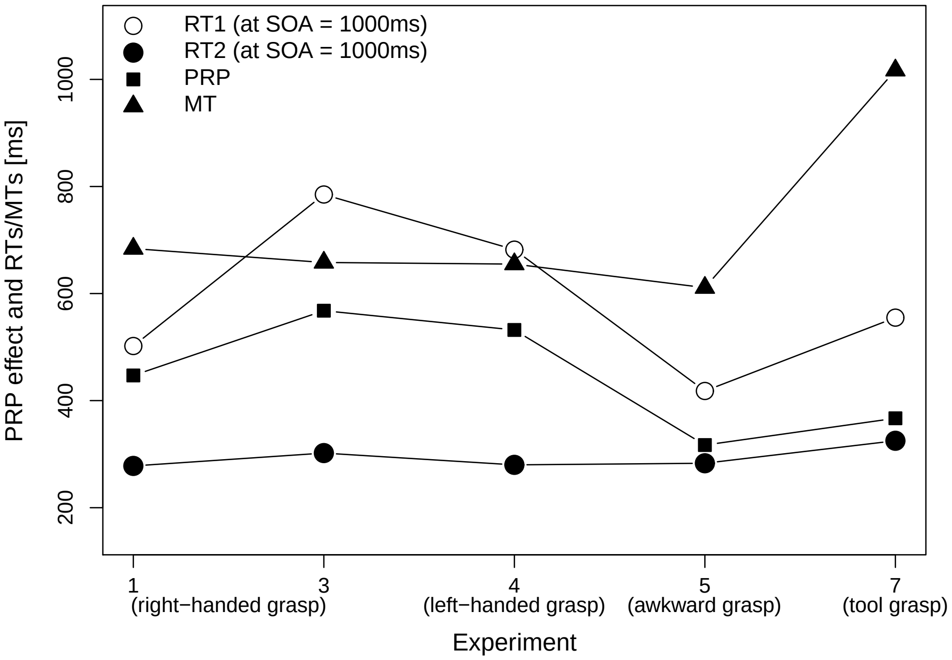

Figure 7.1: Mean response times (RT_1 and RT_2; both at SOA = 1000ms), mean movement times (MT), and the mean PRP effects (calculated according to Equation 3.1) in milliseconds from Experiments 1, 3, 4, 5, and 7.

the grasping types. Then, differences in the size of the PRP effect could be interpreted as indicating varying lengths of grasping central stages. Given that mean RT_2 was almost constant across the grasping tasks (see Figure 7.1; the corresponding ANOVA on RT_2 was non-significant; $F(4, 91) = 1.90$, $p = .12$, $\eta_P^2 = .08$) such an endeavor appears not overly promising. The main effect with MT as the dependent measure; $F(4, 91) = 28.76$, $p < .01$, $\eta_P^2 = .56$; was due to the higher MTs for tool grasping. Indeed, after excluding Experiment 7, the effect was non-significant; $F(3, 60) = 1.23$, $p = .31$, $\eta_P^2 = .06$. Thus, for all hand grasps employed in the present study RTs and MTs were statistically indistinguishable.

On the other hand it is interesting to note that RT_1 differs at all with the various grasping types as T_2. At least in Experiments 1, 4, 5, and 7 T_1 was exactly the same (auditory stimulus – manual key press response) and the central bottleneck model does not predict any influence of T_2 on RT_1. One may attribute this particular finding to between-subjects variations, but nonetheless in Experiments 1 and 7 a similar finding emerged within-subjects: mean RT_1 was longer with perceptual judgment than with grasping as T_2, and the same was reported by Kunde et al. (2007). I will come back to this issue when discussing the theoretical implications of my findings for PRP and dual-task research in the next section.

7.2 Theoretical implications...

Thus far I have reiterated the purposes of the present study and the related empirical results. I will now turn to discussing these results in relation to the Action-Perception Model and PRP/dual-task research.

7.2.1 ...for the Action-Perception Model

The results from the present experiments touch two aspects of the Action-Perception Model. The first is that dorsal and ventral processing apparently both encompass a central processing stage. As a consequence, dorsal processing cannot be construed as automatic as has been suspected by several authors (Enns & Liu, 2009; Goodale & Milner, 2004b; Jeannerod & Jacob, 2005; Liu et al., 2008; Norman, 2002): even simple grasping movements are susceptible to dual-task interference. Secondly, the present results show that skilled right-handed precision grasping on the one side, and left-handed precision grasping or unskilled (awkward and tool) grasping on the other side, seem all being planned and controlled by the dorsal stream – at least based on the absence of Garner-Interference (Ganel & Goodale, 2003). While this contradicts the proposals of Gonzalez et al. (2006, 2008) this also means a step (back) towards parsimony: there is no need to distinguish two classes of target-directed grasping movements, one controlled dorsally, the other ventrally. While this distinction clearly is not at the core of the Action-Perception Model, the results do have another implication: I have mentioned earlier in Section 2.3 that several studies have reported comparable effects of visual illusions on perception and action (e.g., Franz, 2003a; Franz et al., 2001, 2000; 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 (i.e., self-made devices instead of, e.g., the OptoTrak system), such that participants performed an awkward and unskilled movement. As a consequence, grasping should be guided by the ventral stream and therefore would - unsurprisingly - yield the same results as typical perceptual tasks (Goodale, 2008). Note that this argument relies on the one study by Gonzalez et al. (2008), which did not even test this notion directly. In a study directly contrasting the supposedly intrusive devices with non-intrusive devices, Franz et al. (2009) found equal illusion effects with both methods, thereby showing that the counterargument of Goodale (2008) does not necessarily hold true. My result that awkward grasping likely is mediated by the same mechanisms as is right-handed precision grasping further weakens Goodale's argument. Against this background there are no reasons to disregard comparable effects of visual illusions on action and perception as methodological artifacts. This in turn undermines one piece of the main evidence for the Action-Perception Model.

It is necessary to say, however, that both aspects of my results do not question the Action-Perception Model at its core. The Action-Perception Model is basically a neuropsychological and neuroanatomical theory, and the distinction into a vision for action and a vision for perception stream may still hold – even if vision for action is not automatic. The issue of visual illusions has frequently been cited as an important line of evidence for the Action-Perception Model. But even here: the differential susceptibility of action and perception to such illusions is attributed to presumed different spatial coordinate frames (ego- *vs.* allocentric coding) both streams use. Thus, the core theory may still be valid in the absence of this piece of evidence.

7.2.2 ...for PRP and dual-task research

For the PRP/dual-task researcher the present results may come to some disappointment. One of the few reported exceptions from the PRP effect (for a review, see Lien et al., 2006) used microsaccades as responses, an action presumably controlled by specific neural circuits (Pashler et al., 1993). Against this background dorsally mediated grasping movements were another likely candidate for an exception. Yet, the results from the present study counter this possibility, and it appears rather clear that grasping movements cannot be construed as automatic and effortless, and thus are not exceptional in this regard. Indeed, even simple grasping movements that are part of many working environments are susceptible to interference from other tasks.

Let me now come to more puzzling aspects of my data. First, in all grasping conditions mean RT_1 increased with an increasing SOA. Such a finding is neither predicted by the central bottleneck model (predicting no effect of SOA on RT_1; Pashler, 1994), nor by a graded capacity sharing model (predicting decreasing RT_1 with an increasing SOA; Tombu & Jolicoeur, 2003). Thus my data does not allow for distinguishing between both models. I have repeatedly argued that the observed RT_1 increase may be due to response grouping (Miller & Ulrich, 2008) and/or a speed–accuracy trade–off. Still, it is impossible to tell from my data how RT_1 would have behaved without this blurring factors. Moreover, as mentioned above, I observed also a variation of RT_1 depending on the specific nature of T_2, both between-subjects but also within-subjects (in Experiments 1 and 7: grasping *vs.* perceptual judgment as T_2; see also the results reported by Kunde et al. (2007) illustrated in Figure 5.1). It is difficult to reconcile (in particular) this latter aspect with the central bottleneck model (Pashler, 1994; Pashler & Johnston, 1998) where RT_1 is believed unaffected by any T_2 characteristic. Additionally, mean error percentages and RT_2 were higher for perceptual judgment than for grasping, rendering the possibility likely that perceptual judgment was more difficult than was grasping. The difference in RT_2 may be due to increases in all stages, most likely the perceptual and/or central stages. But what about the differences in RT_1? I see two tentative explanations for this particular aspect of my data.

First, a graded capacity sharing model (Tombu & Jolicoeur, 2003) predicts an over-additive effect on RT_1 of (1) manipulations in T_2 pre-central stages and of (2) differences in resource allocation (likely be dependent on T_2 difficulty; see also Tombu & Jolicoeur, 2002, 2003, 2005). A second explanation goes back to Welford (1952) who suggested that response monitoring does also require central capacity. That the central stage is indeed occupied by monitoring R_1 was recently shown by Jentzsch et al. (2007). With the further assumption that a response is only carried out once central resources are freed (e.g., from the concurrent T_2 central processing), such a mechanism also predicts longer RT_1 at short SOAs, hence an overadditive effect. (Note that still it would be unclear how to account for the RT differences at longer SOAs.)

Figure 7.2 illustrates mean RT_1 from my Experiments 1 and 7 and the study by Kunde et al. (2007) as a function of SOA (only 50 and 1000ms) and T_2 (grasping *vs.* perceptual judgment). Numerically the predicted overadditive interaction is present in all three data sets, and significant for Experiment 7; $F(1,31) = 9.06$, $p < .01$, $\eta_P^2 = .23$; and for the Kunde et al. (2007) data; $F(1,23) = 24.75$, $p < .01$, $\eta_P^2 = .52$. Limited by the fact that the interaction in Experiment 7 is mainly due to the increasing RT_1 for grasping as T_2 and the unknown reasons for this (response grouping, speed–accuracy trade–off) the results from this post-hoc analyses may be compatible with both explanations, but at present does not allow distinguishing between them. Clearly, more sophisticated and direct investigations are necessary here.

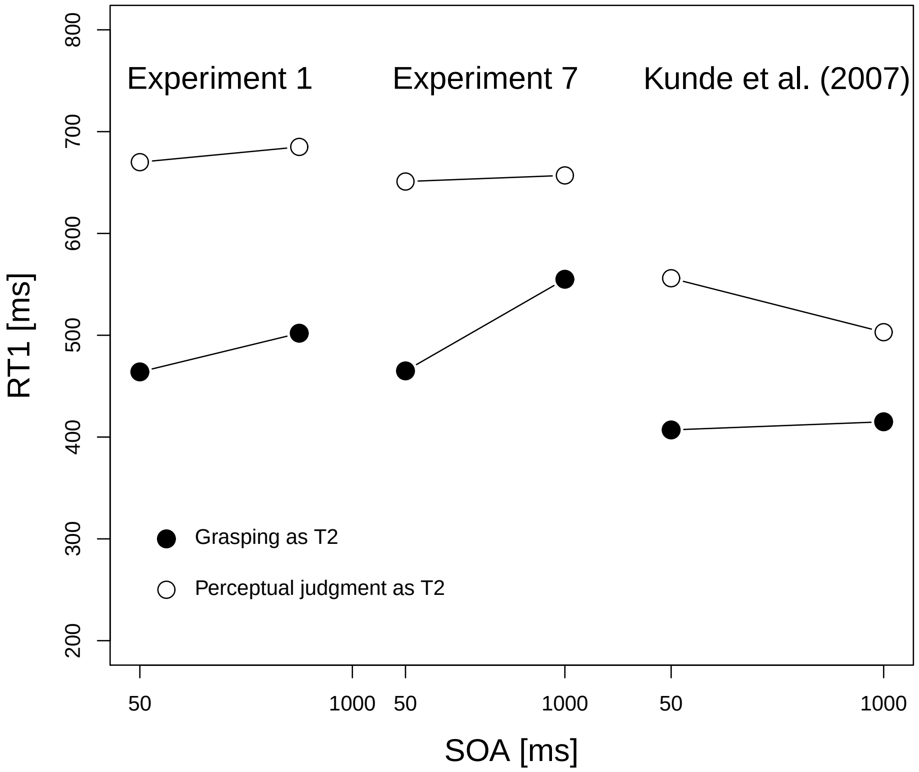

Figure 7.2: Task 1 response times (RT_1) in milliseconds from Experiments 1 and 7 and from the Kunde et al. (2007) study as a function of stimulus onset asynchrony (SOA) and type of Task 2 (T_2).

7.3 Some limitations of the present study

Taking the logic of Ganel and Goodale (2003) seriously, results of Experiments 4-7 require a conclusion different from that of Gonzalez et al. (2006, 2008). In other words: two different indicators of ventral processing suggest two different conclusions. I suspect this being due to the controversial nature of visual illusions. Yet, other explanations exist. First, the present study did not measure kinematic data, but only RTs (and MTs). Franz et al. (2009) have shown that effects typically absent in RT data can indeed arise in kinematic data. I concur that this is possible and cannot be excluded on the basis of my data. Still, Ganel and Goodale (2003) did not find differences in the MGA between baseline and filtering conditions. It is a further problem that only RTs can meaningful be compared to the results from the perceptual judgment task. Secondly, grasping movements in all reported experiments were performed closed-loop (i.e., under full vision). It may thus be that Garner-Interference was blurred by online adjustments in-flight. Again, I cannot exclude this, but still suppose such an interpretation unlikely. In supplementary material, Ganel and Goodale (2003) reported a control experiment where the grasping movements were performed open-loop (i.e., without vision after movement onset). This experiment replicated the closed-loop conditions. A third – and perhaps major – problem is: is the absence/presence of Garner-Interference a valid indicator for an underlying dorsal/ventral processing mode? The link between Garner-Interference and the processing modes is the assumed distinction of analytical (dorsal) and holistical (ventral) processing suggested by Ganel and Goodale (2003). My reading of this latter work is that Garner-Interference is due to a perceptual processing stage, and in PRP experiments this should yield an underadditive interaction of SOA and Garner-Interference (see Chapter 3 or, e.g., Pashler, 1994). In contrast, in my Experiments 1 and 7 and in the study by Kunde et al. (2007) these two factors combined additively, suggesting the implication of (post-)central stages. Garner-Interference may thus be one of the rare perceptual phenomena requiring central capacity (Pashler & Johnston, 1998). Note, however, that baseline and filtering conditions are subject to a potentially important confound: in the baseline condition only two stimulus blocks were used, in the filtering condition four such stimuli. Responses in the perceptual judgment task were always dichotomous, and thus the ratio of stimuli:responses was 2:2 for baseline, but 4:2 for filtering conditions. This increased ratio may have augmented the memory demands and may explain the higher *RT*s for the filtering condition in the perceptual judgment task. Indeed, memory encoding and retrieval have been shown to rely on central stages (e.g., Carrier & Pashler, 1995; Jolicoeur & Dell-Acqua, 1998). Why is the grasping task then unaffected by this confound? I see two possibilities for this. First, the grasping task suggests a more continuous response than the dichotomous response in the perceptual judgment task, and thus the number of stimuli used in each condition may be of less importance to this response mode. Secondly, the dorsal stream (see also Chapter 2) has been described as working in real-time (e.g., Hu & Goodale, 2000; Goodale et al., 2004) and without memory contributions. If this is true, the number of stimuli used in the baseline or filtering conditions should be of no importance at all for the grasping task.

Admittedly, such reasoning undermines the conclusions I made from my Experiments 4-7, but at the very moment the validity of these alternative accounts for Garner-Interference remains to be investigated. As a first step I attempted to deconfound the stimuli:response ratio between baseline and filtering conditions by applying experimental blocks that always used all four stimuli. The rationale of this experiment was as follows: if the ventral system operates on the stimulus blocks holistically the extraction of the relevant dimension (i.e., the width of the blocks) should be more difficult if the relevant and the irrelevant dimension (the length) are more similar. In other words: for a perceptual judgment task, one may expect longer *RT*s for the shorter (63mm) than for the longer stimulus blocks (75mm). For grasping, in contrast, no difference in *RT* may be expected. As is illustrated in Figure 7.3, the results from such an experiment ($n = 32$) exactly match this prediction and are in line with the analytic/holistic distinction (Ganel & Goodale, 2003).

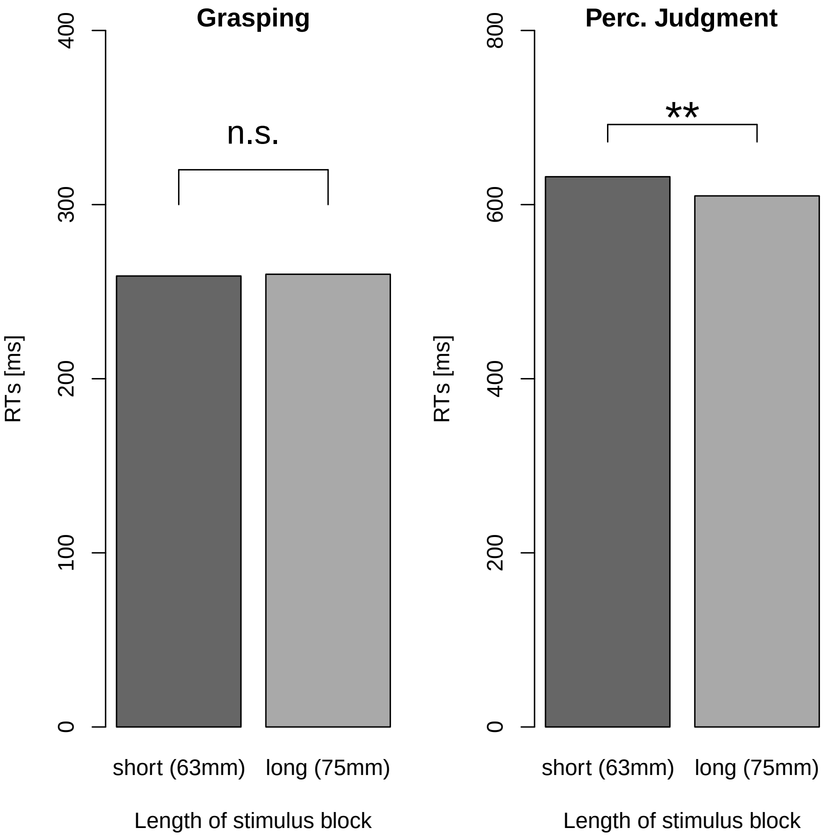

Figure 7.3: Response times (*RT*) in milliseconds from an experiment comparing grasping and perceptual judgments of short *vs.* long stimulus blocks, thus avoiding the potential confound of varying stimulus:response ratios with conditions (baseline *vs.* filtering) in the Garner-Interference paradigm (Note that the two y-axes are scaled differently.).

7.4 Summary and future directions

To summarize, I have presented results from seven experiments in the context of the Action-Perception Model (Goodale & Milner, 1992; Milner & Goodale, 1995, 2006). In light of my results the claim of automatic and effortless dorsal processing is not convincing (Experiments 1-3). Further, distinguishing skilled right-handed grasps from unskilled and/or left-handed grasps seems not necessary. In fact, Garner-Interference was never found (suggesting an underlying dorsal processing mode; Experiments 4-7), and even *RT*s and *MT*s (with the exception of tool grasping *MT*s in Experiment 7) were statistically indistinguishable across my experiments. While these results do not question the basic tenets of the Action-Perception Model – namely the different purposes of the two cortical streams – they nevertheless should help elaborating the Action-Perception Model. In addition, the present results raise some questions and suggest continuing lines of promising future research.

First, given the above considerations, it is necessary to thoroughly evaluate whether Garner-Interference (measured as the *RT* difference between baseline and filtering conditions) is a valid behavioral indicator for the underlying processing mode. If the crucial difference between grasping and perceptual judgment is indeed the response mode (continuous *vs.* dichotomous) one may predict the disappearance of Garner-Interference if the perceptual judgment task requires a more continuous response. A possible way would be to introduce more variation of the stimulus blocks' width and have the participants to judge the width on a larger (and arbitrary) scale to make impossible the dichotomous response mode prone to variations of the stimuli:responses ratio. Secondly, assuming that Garner-Interference is a valid indicator it is tempting to transfer the paradigm to a computer setting. If Garner-Interference can be observed under these circumstances, too, it may be used to study planning and processing characteristics of movements with virtual tools like a computer-mouse or other input devices. Clearly it is important to investigate if (and how) such movements are susceptible to irrelevant variations. Such research would not only help revealing similarities and differences to natural movements, but may also help designing working environments more efficient and ergonomic.

It is needless to say at this point that further research is necessary, but I believe that both the Action-Perception Model and the central bottleneck model are still viable theories from which multiple testable hypotheses can be derived. Regardless of whether they eventually turn out right or wrong – their very heuristic value makes them good theories.

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A Formal predictions from the central bottleneck model

This appendix provides a formal account of relevant predictions that can be derived from the central bottleneck model. First, the case of a T_2 manipulation affecting central processing stages will be addressed, followed by the case in which the T_2 pre-central stage is affected. Finally, I will briefly show the relation of the PRP effect and RT_1. A_i, B_i, and C_i refer to pre-central, central, and post-central stage of Task i, respectively.

A.1 T_2 central stage manipulations

Let M_C denote the duration of a manipulation affecting the T_2 central stage (B_2). Let RT_2 and $RT_{2|M_C}$ denote RT_2 without and with, respectively, this manipulation M_C. Then

$$RT_1 = A_1 + B_1 + C_1$$

For RT_2 two cases need to be distinguished:

1. If the pre-central stage of T_2 (A_2) finishes **before** the central stage of T_1 (B_1) finishes, i.e., $SOA + A_2 < A_1 + B_1$, then

$$RT_2 = A_1 + B_1 + B_2 + C_2 - SOA \tag{A.1}$$
$$RT_{2|M_C} = A_1 + B_1 + B_2 + C_2 - SOA + M_C \tag{A.2}$$

2. If the pre-central stage of T_2 (A_2) finishes **after** the central stage of T_1 (B_1) finishes, i.e., $SOA + A_2 \geq A_1 + B_1$, then

$$RT_2 = A_1 + A_2 + B_2 + C_2 \tag{A.3}$$
$$RT_{2|M_C} = A_2 + B_2 + +C_2 + M_C \tag{A.4}$$

Figure A.1 illustrates this prediction by showing that a central manipulation results in an additive interaction of SOA and M_C.

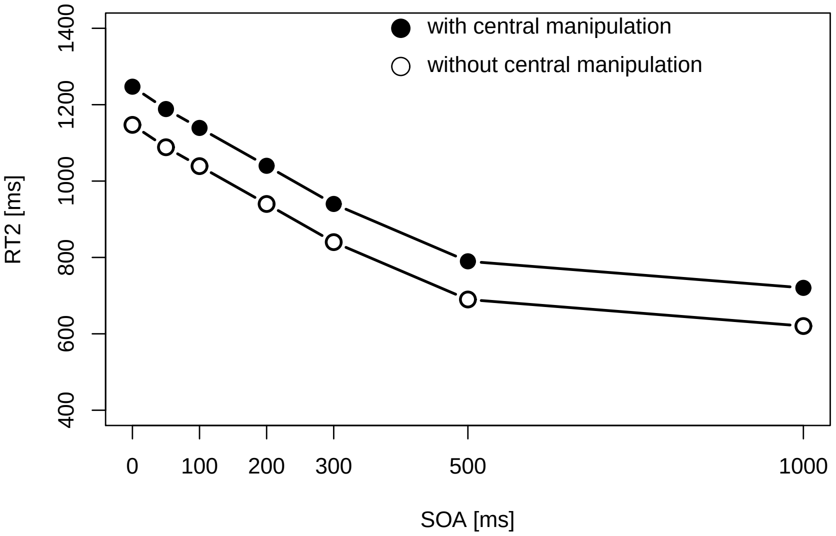

Figure A.1: Simulated Task 2 response times (RT_2) with an additive interaction of SOA and M_C.

A.2 T_2 pre-central stage manipulations

Let M_P denote the duration of a manipulation affecting the T_2 pre-central stage (A_2). Let RT_2 and $RT_{2|M_P}$ denote RT_2 without and with, respectively, this manipulation M_C. Then

$$RT_1 = A_1 + B_1 + C_1$$

For RT_2 three cases need to be distinguished:

1. If the pre-central stage of T_2 with the manipulation ($A_2 + M_P$) finishes **before** the central stage of T_1 (B_1) finishes, i.e., $SOA + A_2 + M_P < A_1 + B_1$, then

$$RT_2 = A_1 + B_1 + B_2 + C_2 - SOA \tag{A.5}$$

$$RT_{2|M_P} = A_1 + B_1 + B_2 + C_2 - SOA \tag{A.6}$$

2. If the pre-central stage of T_2 without the manipulation finishes **before** the central stage of $T_1$1 finishes, i.e., $SOA + A_2 < A_1 + B_1$, but with the manipulation it finishes

after the central stage of T_1, i.e. $SOA + A_2 + M_P \geq A_1 + B_1$, then

$$RT_2 = A_1 + B_1 + B_2 + C_2 - SOA \tag{A.7}$$

$$RT_{2|M_P} = A_2 + B_2 + C_2 + P_M \tag{A.8}$$

3. If the pre-central stage of T_2 without the manipulation finishes **after** the central stage of T_1 finishes, i.e., $SOA + A_2 + M_P < A_1 + B_1$, then

$$RT_2 = A_2 + B_2 + C_2 \tag{A.9}$$

$$RT_{2|M_P} = A_2 + B_2 + C_2 + M_P \tag{A.10}$$

Figure A.2 illustrates this prediction by showing that a pre-central manipulation results in an underadditive interaction of SOA and M_P.

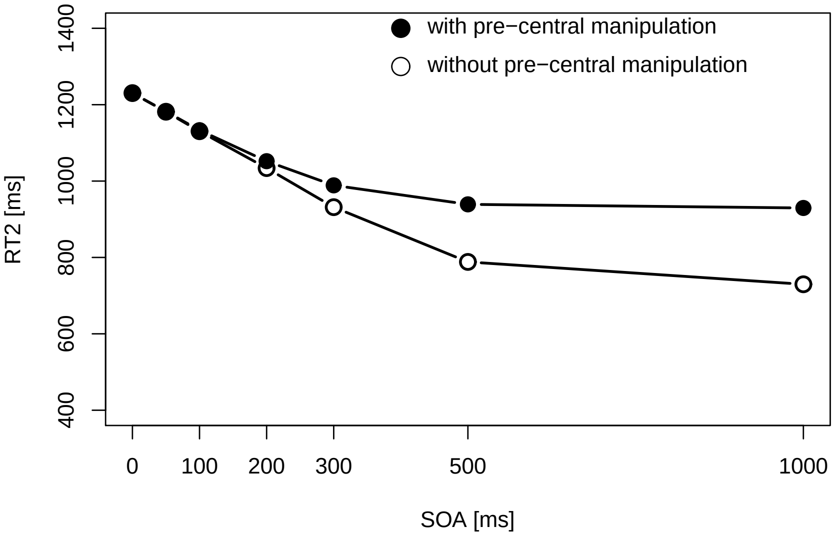

Figure A.2: Simulated Task 2 response times (RT_2) with an underadditive interaction of SOA and M_P.

A.3 Relation of the PRP effect and RT_1

The PRP effect is sometimes calculated as the RT_2 difference between the shortest and the longest SOA, thus

$$PRP := RT_{2|short} - RT_{2|long} \tag{A.11}$$

where (assuming no task overlap at the long SOA)

$$RT_{2|short} = A_1 + B_1 + B_2 + C_2 - SOA \qquad \text{and} \qquad RT_{2|long} = A_2 + B_2 + C_2 \tag{A.12}$$

Substituting Equations A.12 in Equation A.11 gives

$$\begin{aligned} PRP =& (A_1 + B_1 + B_2 + C_2 - SOA) - (A_2 + B_2 + C_2) \\ =& A_1 + B_1 - A_2 - SOA \\ =& RT_1 - C_1 - A_2 - SOA \end{aligned} \tag{A.13}$$

From Equation A.13 it follows that (1) the size of the PRP effect increases with longer RT_1, and (2) that the size of the PRP effect is *not* related to the length of the T_2 central stage (B_2), but only to the length of the T_1 central stage (B_1).

B Detailed RT/MT and %Error results

Table B.1: Mean response times and movement times (MT; only with grasping as T_2) from Experiment 1 in milliseconds as a function of stimulus onset asynchrony (SOA) and condition.

		Task 2					
		Grasping SOA			Perc. judgment SOA		
	Condition	50	500	1000	50	500	1000
Task 1	Baseline	458	497	486	666	616	669
	Filtering	470	514	517	674	678	700
Task 2	Baseline	717	411	274	1029	708	624
	Filtering	734	424	282	1056	774	644
Grasping MT	Baseline	676	679	685			
	Filtering	683	693	689			

Table B.2: Mean percentages of errors from Experiment 1 as a function of stimulus onset asynchrony (SOA) and condition.

		Task 2					
		Grasping SOA			Perc. judgment SOA		
	Condition	50	500	1000	50	500	1000
Task 1	Baseline	2.35	1.19	1.08	2.25	2.10	1.85
	Filtering	1.86	1.44	0.67	3.42	2.73	1.31
Task 2	Baseline	0.26	0.66	1.10	5.56	3.78	3.76
	Filtering	0.91	0.26	0.82	5.88	6.91	7.44

Table B.3: Mean response times (RT), movement times (MT; both in milliseconds), and mean percentages of errors (%Error) from Experiment 3 as a function of stimulus onset asynchrony (SOA) and condition.

		Mean RT/MT SOA			%Error SOA		
	Condition	50	500	1000	50	500	1000
Task 1	Baseline	717	746	778	6.43	4.24	3.93
	Filtering	737	783	797	3.82	3.21	2.50
Task 2	Baseline	856	487	290	2.84	1.32	0.88
	Filtering	884	533	312	1.07	1.87	1.77
Grasping MT	Baseline	640	652	671			
	Filtering	652	666	674			

Table B.4: Mean response times (RT), movement times (MT; both in milliseconds), and mean percentages of errors (%Error) from Experiment 4 as a function of stimulus onset asynchrony (SOA) and condition.

		Mean RT/MT SOA			%Error SOA		
	Condition	50	500	1000	50	500	1000
Task 1	Baseline	593	644	691	4.22	1.83	2.20
	Filtering	597	636	676	3.68	1.97	1.40
Task 2	Baseline	809	455	279	1.19	1.04	0.81
	Filtering	813	452	282	0.66	0.52	0.58
Grasping MT	Baseline	605	608	612			
	Filtering	609	617	616			

Table B.5: Mean response times (RT), movement times (MT; both in milliseconds), and mean percentages of errors (%Error) from Experiment 5 as a function of stimulus onset asynchrony (SOA) and condition.

		Mean RT/MT SOA			%Error SOA		
	Condition	50	500	1000	50	500	1000
Task 1	Baseline	369	388	397	2.64	2.23	1.76
	Filtering	375	406	440	3.24	3.03	2.66
Task 2	Baseline	560	342	285	0.26	0.28	0.70
	Filtering	560	341	281	0.29	0.27	0.54
Grasping MT	Baseline	642	655	650			
	Filtering	655	667	663			

Table B.6: Mean response times and movement times (MT; only with grasping as T_2) from Experiment 7 in milliseconds as a function of stimulus onset asynchrony (SOA) and condition.

		Task 2					
		Grasping SOA			Perc. judgment SOA		
	Condition	50	500	1000	50	500	1000
Task 1	Baseline	454	504	539	636	608	644
	Filtering	475	525	572	667	633	672
Task 2	Baseline	685	425	318	1098	800	712
	Filtering	697	422	331	1181	886	765
Grasping MT	Baseline	1007	1008	1008			
	Filtering	1028	1027	1026			

Table B.7: Mean percentages of errors from Experiment 7 as a function of stimulus onset asynchrony (SOA) and condition.

		Task 2					
		Grasping SOA			Perc. judgment SOA		
	Condition	50	500	1000	50	500	1000
Task 1	Baseline	3.50	2.37	2.27	3.08	1.96	2.35
	Filtering	3.78	2.83	2.04	2.47	1.70	2.16
Task 2	Baseline	3.44	4.10	4.21	6.36	4.45	5.80
	Filtering	4.03	4.27	4.09	9.11	9.14	8.05

C Declaration of authorship

I certify that the work presented here is, to the best of my knowledge and belief, original and the result of my own investigations, except as acknowledged, and has not been submitted, either in part or whole, for a degree at this or any other University.

Eidesstattliche Erklärung

Ich versichere an Eides statt, dass ich die von mir vorgelegte Dissertation selbstständig angefertigt habe und alle benutzten Quellen und Hilfsmittel vollständig angegeben habe.

Eine Anmeldung der Promotionsabsicht habe ich an keiner anderen Fakultät oder Hochschule beantragt.

Teile dieser Arbeit wurden vorab publiziert (genehmigt vom Promotionsausschuss der Fakultät 14 der Technischen Universität Dortmund in seiner Sitzung vom 26.4.2010) als:

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