



Minireview

Attentional landscapes in reaching and grasping

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ABSTRACT

It is well established that during the preparation and execution of goal-directed movements, perceptual processing is biased towards the goal. Most of the previous work on the relation between action and attention has focused on rather simple movements, such as single saccades or manual reaches towards a single target. Here we review recent behavioural and neurophysiological studies on manual actions that require to consider more than a single spatial location in the planning of the response, such as movement sequences, grasping, and movements around obstacles. The studies provide compelling evidence that the preparation of these actions establishes multiple foci of attention which reflect the spatial-temporal requirements of the future action. The findings help clarify how perceptual processing is bound by action preparation and also offer new perspectives for motor control research.

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1. Introduction

All animals with good vision use it to prepare their movements. The brain has therefore often been characterized as a sensory-motor interface that selects visuo-spatial information about the environment and transforms it into goal-directed movements. This is certainly true for the large portion of cortical areas in primates that are involved in visual perception and/or action planning, like the occipital cortex and the fronto-parietal network. Perception and action are functionally and anatomically tightly intermingled and interactive. Together they form a repetitive 'perceive-to-act' cycle, which has its neural basis in a reciprocally interconnected network of visual and motor-related brain structures.

Humans produce a wide variety of visually guided actions, and among these, the motor functions of the hands are exceptionally refined. Here we review recent studies on the selective processing of visual input that is required for the preparation and control of manual reaching and grasping movements. A specific focus of the review will be on the preparation of those types of goal-directed movements in which two or more spatially separate locations are action-relevant and need to be considered in the movement planning, such as in movements around an obstacle, in movement sequences, and in grasping. A central, exciting implication of all this recent experimental evidence is that the preparation of these movements seem to entail the simultaneous deployment of visual attention to several action-relevant locations, forming an "atten-

tional landscape" that closely reflects the requirements of the planned action. The reviewed experiments demonstrate the importance of what we term "visual preparation", i.e. the spatially selective, action-specific extraction of motor-relevant information from the visual scene by means of attentional mechanisms.

Visual preparation involves the top-down weighting of incoming visual information via feedback routes from action planning areas of the brain. We suggest that any kind of goal-directed action preparation is accompanied by a visual preparation process and that the top-down signals that weight visual information at early processing stages may therefore have various possible sources, depending on which motor system is in use. Although understood as a top-down weighting of visual input, the process of visual preparation is automatic in the sense that it is a mandatory component of preparing a goal-directed action. Also, in contrast to deploying attention voluntarily, the spatial resolution of visual preparation and the involved attentional processes depends on the requirements of the motor task (for example see Findlay & Blythe, 2009) and it may not be adjustable by voluntary effort.

We will refer to visual attention in the following as a facilitation or inhibition of the processing of incoming visual information. We prefer to conceptualise these effects in terms of an 'attentional landscape' rather than, for example, an attentional spotlight because during the preparation of movements the visual resources often seem to be distributed in a complex spatial arrangement (we attempted to illustrate this point in Fig. 1A). Although the idea of an attentional landscape contains various aspects of spotlight models, zoom-lens models, and models of differential attentional weights, it describes the parallel weighted facilitation of multiple relevant locations as they structure the workspace. Since movements are prepared quickly, the attentional landscape of a work-

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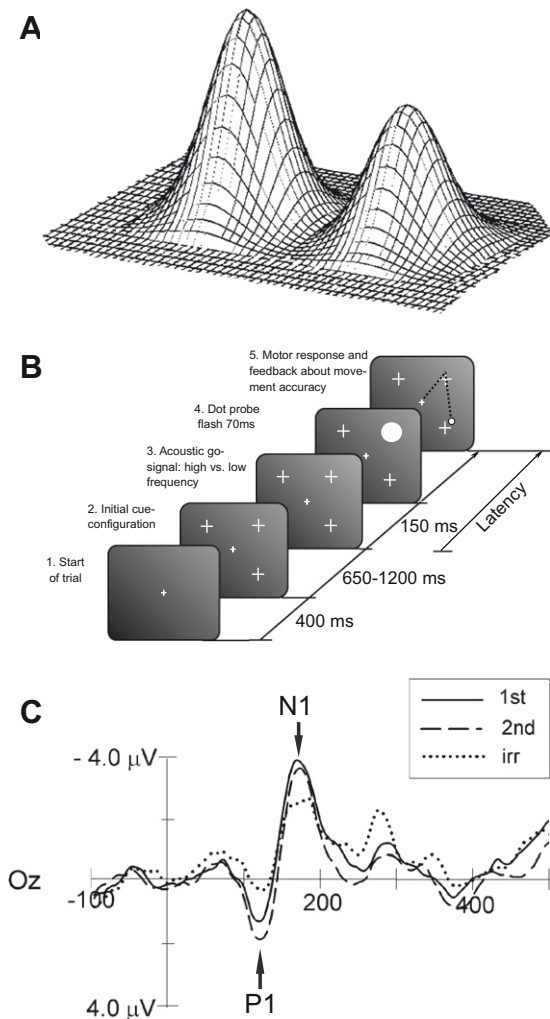


Fig. 1. Selection of multiple reach goals. (A) Schematic illustration of an attentional landscape with multiple foci, which are simultaneously active during action preparation, spatially distinct and weighted according to their relevance for the task. (B) In an EEG experiment, participants were instructed to keep fixation at the central fixation cross. An initial stimulus configuration was presented consisting of three crosses (in the example here the configuration is oriented to the upper right quadrant). A high or low-frequency tone served as the go-signal. Participants were required to execute a speeded double-reach with the first reach being directed to the middle cross of the configuration. Dependent on the pitch of the go-signal, the second reach led to the next position either in a clockwise or a counter-clockwise direction. At 150 ms after the onset of the go-signal, still during movement preparation, a task-irrelevant dot probe was flashed for 70 ms at one of the three cross locations. The dot probe could be flashed either at the first reach goal ('1st') or at the second goal ('2nd') or at the third, movement-irrelevant location ('irr'). (C) Averaged event-related potentials evoked at an occipital electrode (Oz) by the presentation of the dot probe. Dot probes at either the first or second reach-goals elicited larger P1/N1-amplitudes than dot probes at the irrelevant location (adapted from Baldauf & Deubel, 2009).

space will establish quickly and fade or transform itself as soon as a motor goal is achieved.

2. Visual attention and the control of action

Most of the early investigations on visual attention were related to purely perceptual tasks, investigating how attention facilitates the detection (e.g., Posner, 1980) or identification (e.g., Desimone & Duncan, 1995; Treisman & Gelade, 1980) of visual stimuli, or their entry into short-term memory (Duncan & Humphreys, 1989). Allport (1987) and Neumann (1987) were among the first

to point out that – from a functional point of view – spatio-motor actions also rely on selection processes. In natural, complex environments, goal-directed actions—such as the grasping for a certain object in a cluttered scene—involve the selection of the movement goal from many potential targets and the extraction of the visual-spatial parameters relevant for the movement (e.g., the object's position in space, its orientation and its size). These parameters are specific for the intended movement goal and for the required action. Action-irrelevant distractors, such as other objects in the scene, should not interfere. This type of selective processing has been referred to as 'parameter specification' (Neumann, 1987) or 'selection-for-action' (Allport, 1987). Referring initially to saccadic eye movements, Rizzolatti and colleagues (1987) proposed a *pre-motor theory of attention* which stated that covert shifts of attention precede saccades and that covert shifts of attention are actually equivalent to saccadic preparation. To date, there is a good amount of evidence linking selective attention and the planning of saccadic eye movements (Baldauf & Deubel, 2008a; Castet & Montagnini, 2006; Deubel, 2008; Deubel & Schneider, 1996, 2003; Eimer, Forster, Van Velzen, & Prabhu, 2005; Eimer, Van Velzen, Gherri, & Press, 2006, 2007; Hoffman & Subramaniam, 1995; Schneider & Deubel, 2002; Sheliga, Riggio, & Rizzolatti, 1994; van der Stigchel & Theeuwes, 2005, 2006; Wauschkuhn et al., 1998). Also, it is now widely accepted that cortical structures that are activated before oculomotor responses are functionally also involved in covert shifts of attention (for reviews, see Awh, Armstrong, & Moore, 2006; Corbetta et al., 1998; Moore & Armstrong, 2003; Nobre, Sebestyen, & Miniussi, 2000; Perry & Zeki, 2000).

One might suppose that the oculomotor system is so tightly coupled to visual attention because of its specific function to shift gaze to a new object and then to have the eye foveate what has been previously attended. However, motor responses of other effectors also need to be planned on the basis of visual information, although it seems less obvious why the preparation of, e.g., a goal-directed hand movement should influence perceptual capabilities as well. Actually, the premotor theory of visual attention is not explicitly restricted to the attentional preparation of oculomotor responses, but implicates a more general relation between visual attention and any kind of motor preparation (Rizzolatti, Riggio, & Sheliga, 1994). In line with the conjectures of the premotor theory, a number of studies have shown that other goal-directed spatio-motor actions, most prominently hand movements, also involve a deployment of attention to the intended movement goal. In the following we will focus on goal-directed manual movements (for some examples that studied action-related attention for other than hand movements see Hayhoe, Gillam, Chajka, & Vecellio, 2009; Hollands & Marple-Horvat, 2001; Jovanovic, Sullivan, & Hayhoe, 2006; Patla & Vickers, 1997, 2003).

Some of these studies have used *overt* attention, i.e., the eye-fixation behaviour, as an indicator of attention. For example, when observing humans using tools or manipulating objects, Hayhoe and colleagues (Hayhoe, Shrivastava, Mruczek, & Pelz, 2003; Mennie, Hayhoe, & Sullivan, 2007) found a close relationship between the currently performed action and the actor's gaze behaviour: when eye-movements were not restricted actors tended to fixate most of the time at the *goal* of the presently performed motor action (Ballard, Hayhoe, Li, & Whitehead, 1992; Ballard, Hayhoe, & Pelz, 1995; Binsted & Elliott, 1999; Johansson, Westling, Bäckström, & Flanagan, 2001; Land, Mennie, & Rusted, 1999; Neggers & Bekkering, 1999, 2000; Pelisson, Prablanc, Goodale, & Jeannerod, 1986; Pelz & Canosa, 2001; Prablanc, Pelisson, & Goodale, 1986; Smeets, Hayhoe, & Ballard, 1996). In line with this observation, spatial reaching errors increase if actors do not look at the movement targets (e.g., Bekkering, Adam, van den Aarsen, Kingma, & Whiting, 1995; Henriques, Klier, Smith, Lowy, & Crawford, 1998; Neggers & Bekkering, 1999; Vercher, Magenes, Prablanc, & Gauthier, 1994).

Other studies have focused on the coupling of *covert* selective attention and the programming of simple reaching hand movements by analysing either the interference from task-irrelevant distractors (Howard & Tipper, 1997; Tipper, Howard, & Jackson, 1997; Tipper, Lortie, & Baylis, 1992), or the effects visual context can have on the reach kinematics (e.g., Gentilucci, Negrotti, & Ganitano, 1997). In a manual reaching task Deubel and colleagues applied a more direct analysis of the spatial properties of attention allocation by probing perceptual performance at the goal of the intended movement (Deubel, Schneider, & Paprotta, 1998; see also Paprotta, Deubel, & Schneider, 1999). They found evidence that during reach planning, attention is deployed to the movement target and bound to this location until the onset of the movement. In a related approach, Eimer and colleagues measured event-related potentials in response to task-irrelevant visual transients and found that visual attention covertly shifts to the start position of the left or right hand if a manual movement of the respective hand was about to be programmed (Eimer et al., 2006; van Velzen, Gherri, & Eimer, 2006). Recently, Baldauf and Deubel (2009) also provided electrophysiological evidence from an evoked-potential study for prioritised visual processing at the goal of planned reaches. Taken together, all the experimental studies reviewed so far leave little doubt that manual responses also rely on the “visual preparation” of the intended goal location.

3. Parallel selection of multiple goals before sequences of manual actions

Recent investigations have begun to study visual preparation of sequences of goal-directed movements, with surprising results. While the previously discussed studies investigated simple movements directed to a single goal, many goal-directed actions have to consider not only a single movement target but require the processing of several locations or objects for movement preparation. This is the case, for instance, when a fast sequence of goal-directed reaching movements is required. In order to study how attention is allocated in the visual field prior to these more complex actions, we recently extended the previous findings on the goal selection in single reaching movements by studying the deployment of visual attention during the preparation of more complex, sequential motor responses, involving several movement goals (Baldauf & Deubel, 2008a, 2009; Baldauf, Wolf, & Deubel, 2006). Participants were asked to prepare a rapid sequence of reaches to two (or three) peripheral goal locations. While maintaining ocular fixation at the centre of the screen, they first moved the index finger from the screen centre to a location in the periphery that was cued by a central arrow. Immediately after this reach, they moved on with a second reach along the circularly arranged elements to the next-but-one location (in a clockwise direction). Participants were instructed to perform this double-pointing movement as fast and as accurately as possible. Similarly to previous studies, we used a secondary letter discrimination task in order to probe how visual attention is distributed in the visual field during movement preparation, shortly before the initial movement started. It turned out that the perceptual facilitation of action-relevant information was not restricted to the goal of the first upcoming movement. Rather, the data showed significantly enhanced discrimination performance at both the first *and* the second movement goal of the planned sequence, as compared to other task-irrelevant locations. This suggests that the visual attention system is involved in the preplanning of the entire movement sequence in which several movement goals have to be reached serially. In experiments that required triple-sequences of pointing movements, even the third goal was covertly attended well before the first reach component started (Baldauf et al., 2006; see Fig. 2D). Hence, also movement

goals that lie in the rather remote future (i.e., at least some hundred milliseconds ahead) are visually pre-selected if a fluent and rapid motor response is required. Ricker and her colleagues also examined the role of visual preparation in the execution of reaching sequences (Ricker et al., 1999). A full vision condition was compared to conditions in which vision was eliminated during the execution of the first movement component. In line with our findings, their results suggest that the visual processing of the second movement component is completed before the first movement is terminated, and that vision prior to movement onset is used to configure a full movement plan to both targets.

In a recent study, we (Baldauf & Deubel, 2009) added physiological evidence for the parallel selection of multiple goals during movement preparation. We instructed participants to keep their eyes fixated at a central cross (fixation was monitored with an eye-tracker) and to perform speeded double-reaches to two out of three peripheral locations (Fig. 1B). The first reach had to be aimed at the middle cross of the configuration and the subsequent reach was directed to the next position either in the clockwise or the counter-clockwise direction, depending on the pitch of a go-signal. A ‘dot probe’ paradigm was used to map visual attention allocation in the workspace. For this purpose, a visual transient (the dot probe) was flashed during movement preparation at various locations in the visual field. As we had expected from previous work, the dot probe elicited larger P_1/N_1 -components in the ERP signal if it appeared at the first movement goal location as compared to a dot probe appearing at task-irrelevant locations. However, and more interestingly, the probe also elicited enhanced components at the second goal of the planned movement, suggesting that this location in the visual field was also attended.

The finding that multiple movements in a sequence are prepared in advance is also in line with recent studies investigating the chaining of movement components in everyday tasks like dish washing, tea making, etc. (e.g., Hayhoe et al., 2003; Land, 2005, 2006). It has become apparent from these studies that participants who were free to move their gaze proactively prepared their hand movements several steps ahead by “look-ahead” fixations.

These investigations used overt eye shifts as indicators of attention allocation and are compatible with a *serial* model in which selective visual processing occurs ahead of the ongoing action, object by object. Obviously, the oculomotor system is a strictly serial system in that gaze can be directed to only one position in space at a given time. Studying *covert* attention shifts during action preparation however can provide additional information about ongoing selection processes. Indeed, recent investigations have demonstrated that covert attentional mechanisms can distribute processing resources very flexibly and temporally in parallel to several locations. Tereo, Andersson, Flanagan, and Johansson (2002) investigated the control of gaze while encoding several targets for a future reach sequence consisting of discrete target-oriented pointing movements. Interestingly, they found that actors were able to prepare a reach sequence to several locations using peripheral vision only, i.e., without gazing at the targets, if the intended reach goals were isolated from visual distractors. This effective and quick marking of several goal locations was taken as indication that participants encoded the peripheral targets in parallel. That several action-relevant locations are attended in parallel is also well in line with the study by Baldauf et al. (2006). When our participants were asked to prepare a sequential reaching movement, first to a centrally cued position and then to the next position in clockwise direction (see Fig. 2A), it turned out that both intended goal positions were indeed selected in parallel. In this experiment, we implemented a letter comparison task as a secondary task in order to test for the parallel selection of two sequential reach goals. During movement preparation, i.e., briefly after the presentation of the movement cue, two discrimination targets—resembling either the

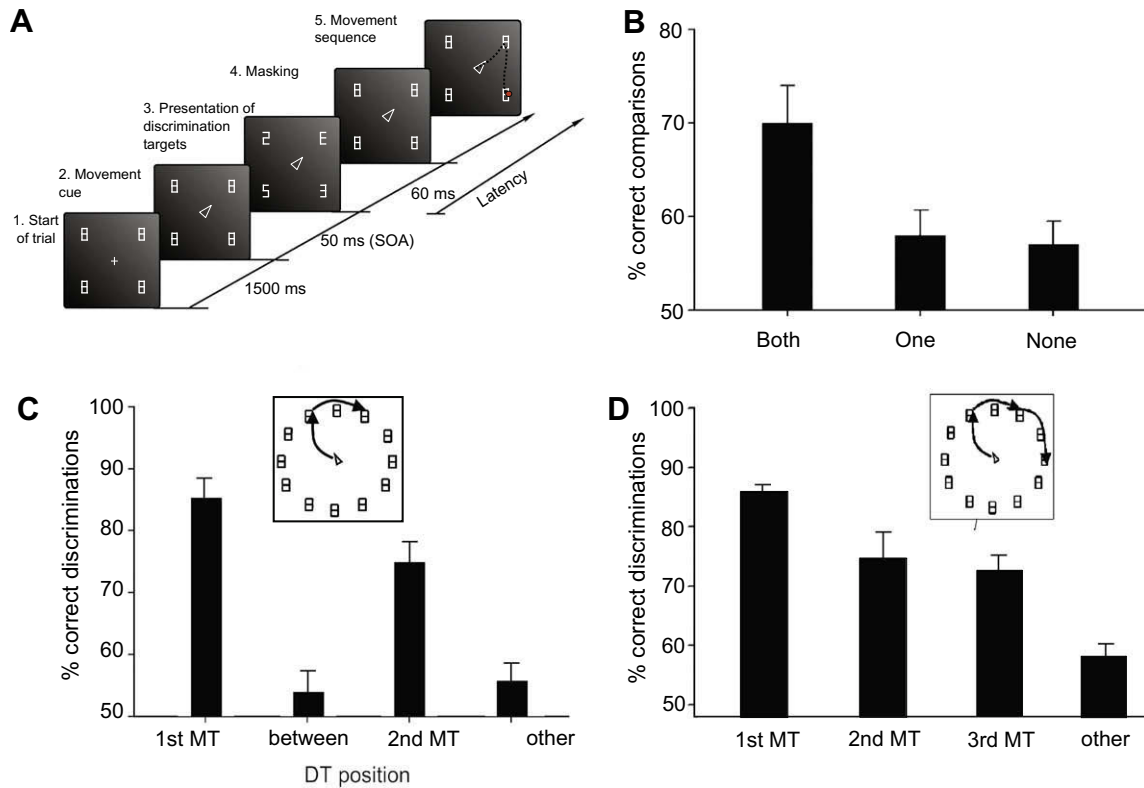


Fig. 2. Parallel attentional selection of sequential goal locations. (A) Sequence of stimuli used by Baldauf et al. (2006). Participants were asked to perform speeded double-reaches to the cued position and to the next position in a clockwise direction. In order to test for the parallel allocation of attention a secondary letter comparison task was employed. During movement preparation, two out of four elements changed for 60 ms into discrimination targets (both resembling either a 'E' or '3'). At the end of each trial, participants responded whether both discrimination targets had been the same or different. (B) Performance in the letter comparison task. The comparison was successful only if *both* discrimination targets coincided with the currently intended movement goals. If one or both discrimination targets were presented at movement-irrelevant locations, the comparison failed. (C) Splitting of attention. When intermediate location between two movement goals were probed it was found that this position was not co-selected with the motor goals. (D) When participants were required to perform triple-reaches, the discrimination of single target letters was increased at all three intended movement goals. The more remote the goal lay in the future the less attention was deployed to the respective position (all adapted from Baldauf et al., 2006).

character 'E' or '3'—appeared at any two of the four peripheral positions. The remaining two positions showed other irrelevant distractor letters (resembling digital '2's and '5's). After a presentation time of only 60 ms all stimuli were masked. At the end of each trial the participant had to indicate whether both discrimination targets had been the same or different. Importantly, this letter comparison task in combination with the short presentation time ensures that the comparison of both discrimination letters can be successful only if both respective locations are selected simultaneously, ruling out averaging artefacts or a fast switching of the attention focus. The data indeed showed that the participants were able to compare the two discrimination targets within 60 ms, but only if *both* of the discrimination targets appeared at the two movement goals of the actually planned double-reach (Fig. 2B). This speaks in favour of a *parallel* model of visual attention where visual resources are flexibly assigned to various locations in the field.

Another interesting finding of the study of Baldauf et al. (2006) was that the spotlight of attention appeared to split into multiple, spatially distinct attentional foci in order to select several future goal locations. When probing discrimination performance at a location in between both movement goals the perceptual performance was close to chance level, just as it was at other task-irrelevant locations in the scene (Fig. 2C, see also Baldauf & Deubel, 2009). This remarkable result shows that attention is dividable, at least under conditions in which selective attention is employed in action preparation, and in which spatially accurate movements must be planned towards two (or more) distinct locations. In the domain of purely perceptual tasks it has been debated over dec-

ades whether the attentional spotlight can be split among several locations (for an excellent review see Cave & Bichot, 1999). In the above described experiments the selected targets and the intermediate, non-selected locations were separated by about 3 deg of visual angle only. Therefore, the finding of spatially distinct, simultaneously active foci of visual attention allows some rough quantification of the spatial resolution of the involved selection-for-action processes. Apparently, the attentional landscape consisting of various distinct attention peaks can be high-resolving if the tasks requires it, e.g., if close-by or intermediate non-targets have to be avoided (see also Findlay & Blythe, 2009).

Unfortunately, not much is known about the *dynamics* of the attentional landscapes before and during goal-directed manual movements. However, there are recent studies on the time course of attention shifts before saccadic eye movements which showed that the attention focus shifts to the saccade goal in a time interval of about 100 ms, immediately before the saccade onset (Deubel, 2008; Montagnini & Castet, 2007). We assume that the temporal development of the multiple attentional foci discussed before has similar dynamics, which is in line also with findings from neurophysiological studies discussed in more detail below.

The view of flexibly adapted visual resources in action preparation has received further support from several studies that described a *spatial gradient* of attentional weights, with more visual resources being deployed to positions that are more important from a motor-planning point of view (Baldauf, Cui, & Andersen, 2008; Baldauf & Deubel, 2008a, 2008b; Baldauf et al., 2006). When complex manual reach sequences require the parallel preparation of multiple goal positions it was observed that the immediate

goals, i.e., the targets relevant for the impending movement, received more visual attention than subsequent ones, even though all goals were equivalently significant for the task. In triple reach sequences this gradient followed a linear trend, with the least amount of resources being dedicated to the third goal (Baldauf & Deubel, 2008a; Baldauf et al., 2006; see Fig. 2D). Furthermore, the way visual attention is distributed during motor planning does not only mirror the locations of the action-relevant targets, but seems to also reflect the spatial acuteness and temporal contiguity of the intended movement (see also Ansuini, Grigis, Massaccesi, & Castiello, 2009). In this respect, Baldauf et al. (2008) observed that the relative attentional weighting of the primary versus secondary movement goal was reversed when the behavioural difficulty of motor target acquisition was manipulated. When subsequent goals had to be acquired after a longer delay and no visual landmarks regarding the second goal location were given, these secondary movement goals became rather hard to reach accurately. As a consequence, the strength of representation of both movement goals in parietal populations reversed as well, with even more resources now being deployed to the second as compared to the first goal (Baldauf et al., 2008). In a follow-up study, Baldauf (2009) investigated visual preparation in reaching sequences as a function of the sequence timing. It was found that in rapid sequences with inter-reach delays shorter than 400 ms, a subsequent second goal was indeed attended before the onset of the movement sequence. In trials with longer inter-reach delays, however, the visual system solely prepared the immediate goal of the first movement of the sequence. This indicates that movement components are bound together and become integrated into one common action plan only if the delay between the movement components is short. Aivar and colleagues (Aivar, Brenner, & Smeets, 2005) analysed the movement kinematics when human actors executed visually guided double-reach sequences in which sudden changes to the appearance of either the first or second target occurred during movement execution. They observed significant increases of the inter-reach dwell time and concluded that fast movement sequences are treated as a single action even if there is an intermittent target (for the binding of action sequences on a longer time scale, see Ansuini et al., 2009). In the field of movement kinematics, the phenomenon of “chunking” of individual reaching movements into one common action plan has often been observed (Adam & Paas, 1996; Adam, van der Bruggen, & Bekkering, 1993; Adam et al., 1995; Khan, Mourton, Buckolz, & Franks, 2008). Together, the findings demonstrate that the properties of attention deployment reflect both timing and accuracy demands of complex movements in an amazingly specific manner.

Multiple movement goals occur not only in sequential actions but also, for example, when we manipulate objects bimanually. When studying visual attention in bimanual motor tasks, it again became apparent that overt and covert attentional mechanisms might work together. For example, Riek and colleagues (Riek, Tresilian, Mon-Williams, Coppard, & Carson, 2003) investigated overt attention shifts in a task where the participants bimanually reached to two locations. They observed a sequence of gaze shifts between both target locations until both index fingers finally landed on the respective goals. In a recent study, we probed covert attention by asking participants to execute similar bimanual reaches while the eyes were on a central fixation and observed that both movement goals were attended in parallel (Baldauf & Deubel, 2008b). By comparing the perceptual performance at the goals of the left and right hand, we found more visual attention to be deployed to the location that was farther away from the starting point and therefore was more difficult to reach. So, also here, the pattern of attentional allocation seemed to be sensitive to the specific demands of the motor task.

Another example of a complex reaching task that involves multiple movement goals was recently studied by Collins and col-

leagues (Collins, Schicke, & Röder, 2008), who investigated visual attention in a reaching task involving tool use. They designed a triangularly shaped tool that participants had to use to point to a goal location. The design of the experiment allowed the dissociation of the allocation of attention at the motor goal of the movement (i.e., at the end position of the effector) and at the intended spatial goal of the movement (i.e., the endpoint of the tool tip). Collins et al. showed that also in this task, visual attention splits and selects both movement goals in parallel: the goal of the tool tip as well as the final position of the hand. The results imply that for the selection of multiple movement goals it does not matter whether two movement components are executed simultaneously or serially, as long as all the involved movement goals are behaviourally relevant during the preparation period.

Taken together, these studies set the ground for analysing more complex aspects of visual movement preparation. The findings imply that the need to consider multiple movement goals in the preparation of an action does not overburden the visual system since covert attention mechanisms can – in contrast to the oculomotor system – select several locations in parallel if required by the motor task. Also, the amount of attentional resources that are allocated to the various goals seems to be highly flexible, depending on the specific demands of the motor task.

Of course, however, we cannot prepare an arbitrary number of movement goals at once – clearly there must be an upper limit. Therefore, the fact that several intended movement goals (i.e., at least three of them) are prepared in parallel by multiple foci of visual attention is fascinating also from another point of view: for quite a while researchers have put forward the hypothesis that visual attention and working memory are interrelated functions. Smyth and Scholey (1994), for example, argued that the maintenance of spatial memory involves covert shifts of attention (see also Smyth, 1996). Awh, Jonides, and Reuter-Lorenz (1998) also tested the proposed relationship and indeed observed facilitated visual processing at the location they had to hold in memory. Already Baddeley conceptualised a connection between the rehearsal in working memory and hidden action plans. In his influential working memory model he proposed that the spatial component of visual memory (the so-called visuo-spatial sketchpad) may be based on the implicit preparation of eye movements (see Baddeley, 1987, pp. 116–121). Awh, Anillo-Vento, and Hillyard (2000) showed that task-irrelevant visual transients elicit very similar event-related EEG-components whether participants are involved in a spatial attention task or a spatial memory task (further studies were reviewed by Awh and Jonides (2001), and by Theeuwes, Belopolsky, and Olivers (2009)). Therefore, also physiologically, the involved networks seem to overlap to a considerable degree (see below in the section on the neural substrate of selection-for-action). This striking connection between visual attention and visual working memory is further supported by the experiments of Smyth and Pelky (1992), who demonstrated that spatial working memory is affected by goal-directed manual reaches (see also Hale, Myerson, Rhee, Weiss, & Abrams, 1996; Lawrence, Myerson, Oonk, & Abrams, 2001). Chum and colleagues showed that spatial arrays were better remembered if participants actively pointed at the individual items with their index fingers during the encoding phase – compared to solely passive visual observation (Chum, Bekkering, Dodd, & Pratt, 2007). Apparently, perceptual encoding of visual stimuli is improved if accompanied by planning motor actions to those stimuli. Given the similarities of working memory and action preparation, it would be interesting to test whether there is a maximum ‘magical number’ of movement goals that can be prepared by visual attention in parallel, possibly about four (Cowan, 2001). Oksama and Hyönä (2004) recently tested in a large group of participants how many individually moving objects they could track simultaneously. On average they also found a limit of four ob-

jects, although capacity varied between subjects and it is hard to tease apart limitations that stem from memory versus tracking processes (see also Cavanagh & Alvarez, 2005; Pylyshyn & Storm, 1988).

4. Visual preparation of grasps

Grasping an object seems to be a straightforward exercise which at least adults perform with ease. But considering how long it takes humans to optimise this skill may give a hint that visually guided grasping is not an easy but a highly complex type of action (Kuitz-Buschbeck, Stolze, Jöhnk, Boczek-Funcke, & Illert, 1998; Rösblad, 1997; Schneiberg, Sveistrup, McFadyen, McKinley, & Levin, 2002). The generation of stable grasps, i.e., grasp types that are appropriate to the respective object and avoid collisions or slipping, is a largely unsolved problem in the field of robotics, particularly if the grasp is solely based on visual information (Corke, 1993; Hashimoto, 1993; Hauck, Rüttinger, Sorg, & Färber, 1999; Schenck, Hoffmann, & Möller, *in press*). With respect to selective visual processing, grasping seems to be specifically challenging since here again multiple movement goals – the future points of finger application – need to be considered in movement preparation. Smeets and Brenner (1999) emphasized this point by a model that conceptualised grasping to be similar to reaching with the thumb and index finger separately to selected positions on the surface of an object. Another aspect that makes visually based grasping more challenging than simple reaching is the fact that additional information about the object's features, such as its presumed weight and its centre of gravity, becomes relevant during grasp preparation. Finally, visual processing comes again into play at the very end of the movement when visual feedback needs to be integrated for the final, closed-loop movement control (Binsted, Chua, Helsen, & Elliott, 2001; Lünenburger, Kutz, & Hoffmann, 2000).

Johansson and co-workers were among the first to study *overt* selection during grasping (Johansson et al., 2001). Their participants initially had to grasp a bar and then to use it in order to press a switch without colliding with an obstacle along the transportation path. Similar to the findings on gaze behaviour in more natural tasks (Aivar, Hayhoe, Chizk, & Mruzeczek, 2005; Hayhoe, 2000; Land & Hayhoe, 2001; Land et al., 1999), Johansson et al. reported that actors always directed their gaze to the positions they were about to make contact with, such as the application points on the bar or the final movement target. Locations, which they had to actively avoid, like the obstacle, were also fixated in almost every trial. However, with respect to the grasping component, Brouwer, Franz, and Gegenfurtner (2009) correctly pointed out that in the task set-up of Johansson et al., only one point of application was visible to the actor, while the second contact point was hidden in the back of the object. From this point of view, the study of course could not resolve the question which surface *parts* of an object are visually selected before or during grasping movements. Therefore, Brouwer and colleagues investigated in a follow-up study the fixation behaviour of human actors during grasping under conditions where all potential points of application were clearly visible to the actor (see Fig. 3).

One particularly interesting result of their study was that oculomotor behaviour in a grasping task was different from gaze control in a free-viewing condition without grasping. The differences manifested as early as at the second fixation in each trial, which usually started long before the hand actually touches the object's surface. Under no-grasping conditions these saccades landed closer to the object's centre of gravity, whereas in grasping trials the gaze was directed closer to the object's edges. In a second experiment, Brouwer and co-workers let participants grasp geometrical objects with

the thumb and index finger of either the right or left hand. The results suggested that under these conditions gaze landed consistently on one of the planned contact points. (see Fig. 3B). Hardly any gaze switching between both contact locations was observed. Interestingly, participants preferentially fixated on the application point which was more difficult to make contact with and at which more visual feedback was needed, e.g., at the small tip of a triangle (see Fig. 3C) rather than its base (see also de Grave, Hesse, Brouwer, & Franz, 2008).

These findings provide evidence for the hypothesis that overt eye movements in grasping preferentially select those parts of an object at which visual feedback is needed (see also Binsted et al., 2001). But, as Brouwer et al. (2009) pointed out, the gaze can only be at one location at a time. The time needed to initiate the reach-to-grasp movement is probably too short as to sequentially scan the object's surface. Interestingly, in Brouwer et al.'s study also the centre of gravity (COG) of the object had an effect on the distribution of gaze landings: the initial saccade to the object was often directed to the COG, and even secondary saccades were still biased towards the COG. Two explanations may account for this observation. First, the tendency to fixate the COG may result from a spatial averaging process. Indeed, it is well-known from eye movement research that saccades are often found to be directed to an intermediate position between two items that are presented in neighbouring locations. This centre-of-gravity effect (Deubel, Wolf, & Hauske, 1984; Findlay, 1982) was interpreted to indicate that processes of low spatial resolution are operative in overt attentional control. However, while spatial averaging seems to be the default option when a fast response to a newly appearing stimulus configuration is required, more recent research has demonstrated that longer-latency saccades can target a location accurately while ignoring adjacent visual distractors (Findlay & Blythe, 2009; see also He & Kowler, 1989). Since in the Brouwer et al. (2009) study the target objects were visible long before the start of the eye and hand movement to the target, it is unlikely that spatial averaging prevented spatially accurate saccades. As a second explanation, fixation of the COG of the to-be-grasped object may be the result of a deliberate strategy. Indeed, the COG is a convenient location for viewing the object during grasping preparation. It may allow to distribute covert attention effectively to the grasp points of the object. Also, it is known that this location is behaviourally important for the effective manipulation of the object; for example, it has been shown that precision grasps are only successful (i.e., stable) if the COG lies between both points of application (Iberall, Bingham, & Arbib, 1986; Mac Kenzie & Iberall, 1994).

Only few studies have directly probed *covert* visual attention in grasping. They support the hypothesis that there is more selected than just one of the (at least) two points of finger application. In a dual-task paradigm, Castiello (1996, 1999) let participants grasp fruits and simultaneously count how often a peripheral distractor object was illuminated. He observed that the size of the distractor influenced the aperture of the ongoing grasp movement, indicating that the size of the to-be-grasped object was also covertly attended. In trials without the secondary counting task, participants successfully ignored surrounding distractors and the hand movement kinematics remained unaffected (see also Castiello, 2001). In a study by Bonfigliani and Castiello (1998) participants had to covertly track a moving distractor in the periphery while grasping for a target object. The allocation of covert attention to the moving stimulus affected the transport component of the reach-to-grasp movement. In a subsequent experiment, Kritikos, Bennett, Dunai, and Castiello (2000) varied the size of the distractor that had to be attended covertly and found that the distractor's size also interfered with the manipulation component of an ongoing grasp, in particular with the maximal aperture of the hand. Craighero, Fadiga, Rizzolatti, and Umiltà (1999) reported that a quick preview

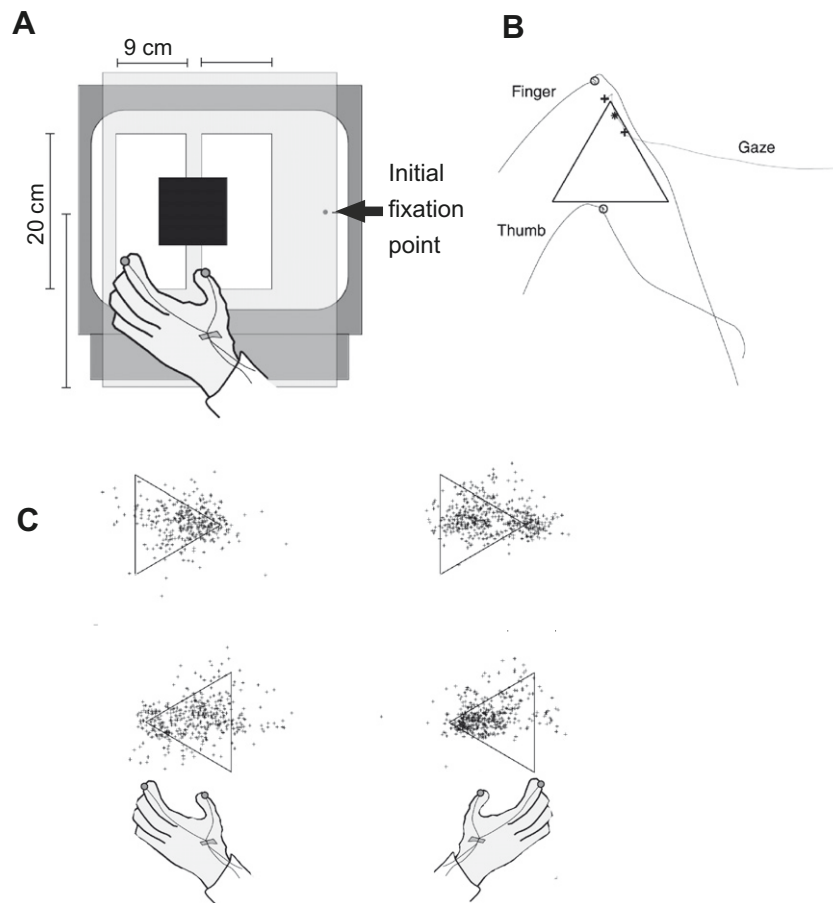


Fig. 3. Overt selection of to-be-grasped objects. (A) Experimental set-up used by Brouwer et al. (2009), for studying the gaze behaviour during visually guided grasping of geometrical objects. At the beginning of each trial an initial fixation point was presented to the left or right of the to-be-grasped stimulus. (B) Example of the gaze orientation when grasping an upright triangle along its vertical axis. The curved lines represent the movement trajectories of finger and thumb and of the eyes, respectively. The eyes preferentially selected the intended contact point at the top of the shape rather than the one at its base. (C) In a second experiment participants were instructed to grasp objects along their horizontal axes either with their right or left hand. The four panels show the spatial distribution of eye fixations (indicated by small dots) that accompanied the grasping for differently oriented triangles. The fixation patterns show that there is a tendency to overtly select the smaller of two application locations (e.g., the tip of the triangle), where the contact with the object needs to be more precise (adapted from Brouwer et al., 2009).

picture of an object could prime the preparation of a grasping movement to it. Participants performed the grasps faster if they saw a picture of the same objects that they had to grasp. The authors found similar priming effects for the orientation of graspable bars. Ellis and Tucker (2000) asked participants to perform a power or precision grip depending on which of two acoustic tones was presented. Simultaneously, they viewed an object that would normally be grasped with either a power or a precision grip. The results showed strong interference of the instructed task from the affordance of the seen object (however see Cant, Westwood, Valyear, & Goodale, 2005). Lindemann and co-workers (2006) showed how action preparation could be supported, i.e. speeded up, by reading words that are consistent with features of the concurrently prepared action. This adds a more general semantic component to the selection-for-action hypothesis. Such visuomotor priming is also effective in the reversed direction: preparing a certain motor action can facilitate the visual processing of objects that are compatible with that action (see Bekkering & Neggers, 2002; Hannus, Cornelissen, Lindemann, & Bekkering, 2005; Müsseler, Steininger, & Wühr, 2001).

Schiegg and colleagues (Schiegg, Deubel, & Schneider, 2003) directly probed the spatial and temporal properties of covert visual attention when participants were required to grasp a wooden cross with their thumb and index finger (see Fig. 4A). The participants were asked to keep fixation on the object's centre. Visual probe

stimuli were projected via a mirror set-up onto the action plane; they changed into discrimination targets during the movement preparation period. Upon an acoustical go-signal, participants had to grasp the cross either with their right or left hand, depending on the pitch of the stimulus.

When using the right hand, the thumb touched the lower left branch end and the index finger touched the upper right branch end. When using the left hand the respective opposite branch ends were to be contacted. With a SOA of 150 ms after the go-signal, one of the projected mask elements changed into a symbol resembling either a 'E' or a '3' whereas all other mask elements changed into irrelevant distractors. All probe stimuli were post-masked after 140 ms, i.e., well before the actual reach-to-grasp movement started. After completing the appropriate grasp participants had to indicate the identity of the character. Discrimination performance in this secondary letter discrimination task served as a measure for the deployment of visual resources in the field of action (see Fig. 4B). The results revealed a significantly enhanced discrimination performance in those trials in which the discrimination target was presented close to an intended point of application, as compared to trials in which the discrimination target was presented at the opposite, not-grasped ends of the object branches. Perceptual performance at both points of application was improved compared to control experiments in which no grasping movement had to be executed. The spatially selective processing

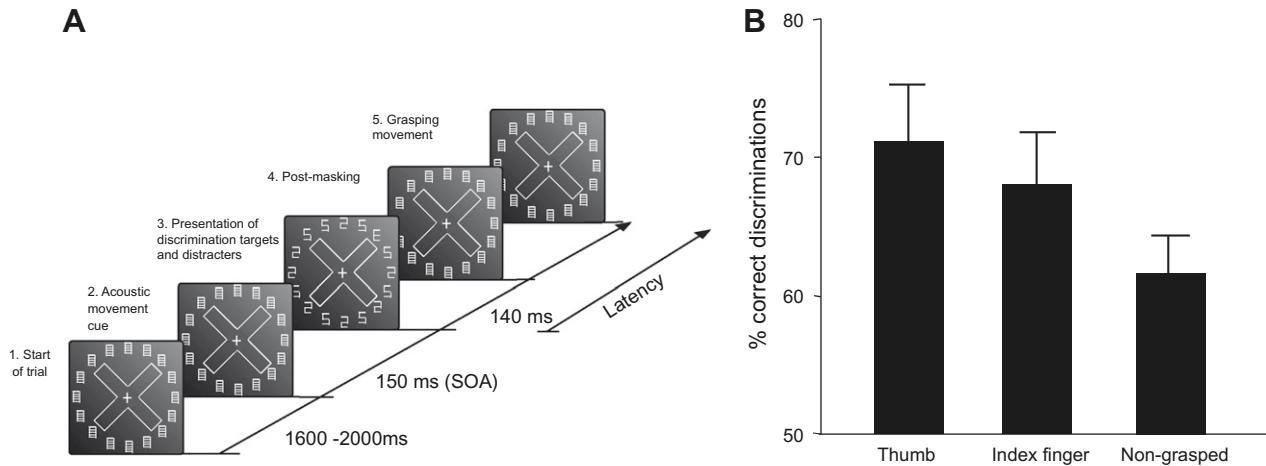


Fig. 4. Covert selection of to-be-grasped objects parts. (A) Sequence of stimuli in an experiment by Schiegg et al. (2003) to map visual attention at various surface points of a cross-shaped, to-be-grasped object. Before the reach-to-grasp movement was initialised, 150 ms after the onset of the go-signal, a discrimination stimulus ('E' versus 'Э') was briefly presented at a random position among distractors. At the end of the trial, after the grasp was completed, participants had to indicate the identity of the discrimination stimulus. Discrimination performance at the various positions served as measure for the allocation of visual attention. (B) Discrimination performance at the intended points of application for the thumb and the index finger was superior to the discrimination performance at the other, action-irrelevant points of application (adapted from Schiegg et al., 2003).

at the intended application points could be observed even if the participant was informed about the location at which the discrimination target was to be presented. This was interpreted as evidence for an obligatory coupling of prehension movement preparation and visual attention: it seems hardly possible to attend to a certain location on an object while preparing a grasp movement to other areas of the very same object. Interestingly, this study shows (in some contrast to the overt selection processes that Brouwer et al. (2009) reported during grasp preparation) that *both* points of application were selected covertly. This result fits into the picture that covert attention can be split and flexibly arranged to the needs of the current motor task – which is of course not possible by overt attention mediated by eye movements.

Presumably, what is usually referred to as 'grasping' comprises distinct phases of an action. Grasping an object starts with a reach-to-grasp movement (or 'transportation phase', see e.g., Bonfiglioli & Castiello, 1998) that brings the hand close to the object of interest, followed by – or passed into – a second phase in which the appropriate grasp type is formed and the movement is piloted to the prepared points of application (Smeets & Brenner, 1999, called this the 'grip component'). In a manipulation phase, finally, the grasp is stabilized and grip forces are continuously adjusted to compensate for the changing forces of gravity. Along this evolving temporal sequence, visual attention could play different roles such as target selection for the initial reach component, followed by the selection of more specific grasp application points, and finally the selection of relevant object features such as its centre of gravity. Droll and colleagues studied change detection in various stages of a virtual manipulation task (Droll, Hayhoe, Triesch, & Sullivan, 2005). They found that the actors' ability to detect changes to the visual appearance of the currently manipulated virtual objects altered dramatically over various manipulation phases such as the pick-up, the transportation, or the put-down of objects. Future studies of covert visual attention in grasping are required that focus on the temporal dynamics and the continuously changing function of visual selection processes during the course of the grasp.

5. Reaching and grasping in cluttered scenes: avoiding obstacles

In natural tasks, we usually do not act on isolated objects but often in cluttered or even crowded visual lay-outs. Several studies suggest that non-target objects strongly influence the attentional

preparation as well as the execution of reaches and grasps, showing that not only the final goal location of a reach is selected by visual attention, but also non-targets, given they are movement-relevant. Especially during the initial reach-to-grasp component, the presence of an obstacle poses an important additional burden for the visual preparation and the motor programming of a successful grasp (e.g., Castiello, 1996, 1999; Mon-Williams, Tresilian, Coppard, & Carson, 2001; Tipper, Meegan, & Howard, 2002; Tipper et al., 1997; Tresilian, 1998, 1999; Tresilian, Mon-Williams, Coppard, & Carson, 2005). Tresilian (1998) emphasized that obstacles in movement tasks often do not fit the definition of 'distractors' because they are not, from the viewpoint of programming the movement, irrelevant to the task but rather constitute spatial constraints on the execution. He showed that people generally keep their hands outside of a region that surrounds the obstacle by a minimum preferred distance (see also Dean & Bruwer, 1994). Tipper and colleagues described an 'attentional repulsion' effect showing that reach trajectories deviate away from non-target objects which were attentionally inhibited (Howard & Tipper, 1997; Tipper et al., 1997), including purely visual stimuli without substantial physical extension such as an illuminated LED (see Fig. 5A). Tipper and colleagues (Tipper et al., 1997) proposed that the involved attention system must represent more than just the target object for action. Using a similar approach, Chapman and co-workers (Chapman et al., 2007) found stronger activation of reach-related areas in the parietal cortex (specifically in the precuneus, a human homologue to the parietal reach region in monkeys) when non-target objects were present during reach movements.

Several studies have shown in grasping tasks that the initial reaching component is prolonged if an obstacle is present as compared to the same movement executed without any obstacles (Biegstraaten, Smeets, & Brenner, 2003; Jackson, Jackson, & Rosicky, 1995; Jaric, Tortoza, Fatorelli, & Almeida, 1999; Mon-Williams & McIntosh, 2000; Mon-Williams et al., 2001; Saling, Alberts, Stemach, & Bloedel, 1998; Tresilian, 1998), which can be taken as evidence for the additional need of anticipatory programming. Also the maximum grip aperture during the initial transportation phase was shown to be smaller when the grasping movement was performed around an obstacle (Jackson et al., 1995; Mon-Williams et al., 2001; Saling et al., 1998; Tresilian, 1998). Presumably, minimizing the aperture of the moving hand is a clever strategy to minimize the risk of collision with the obstacle while the hand is in flight.

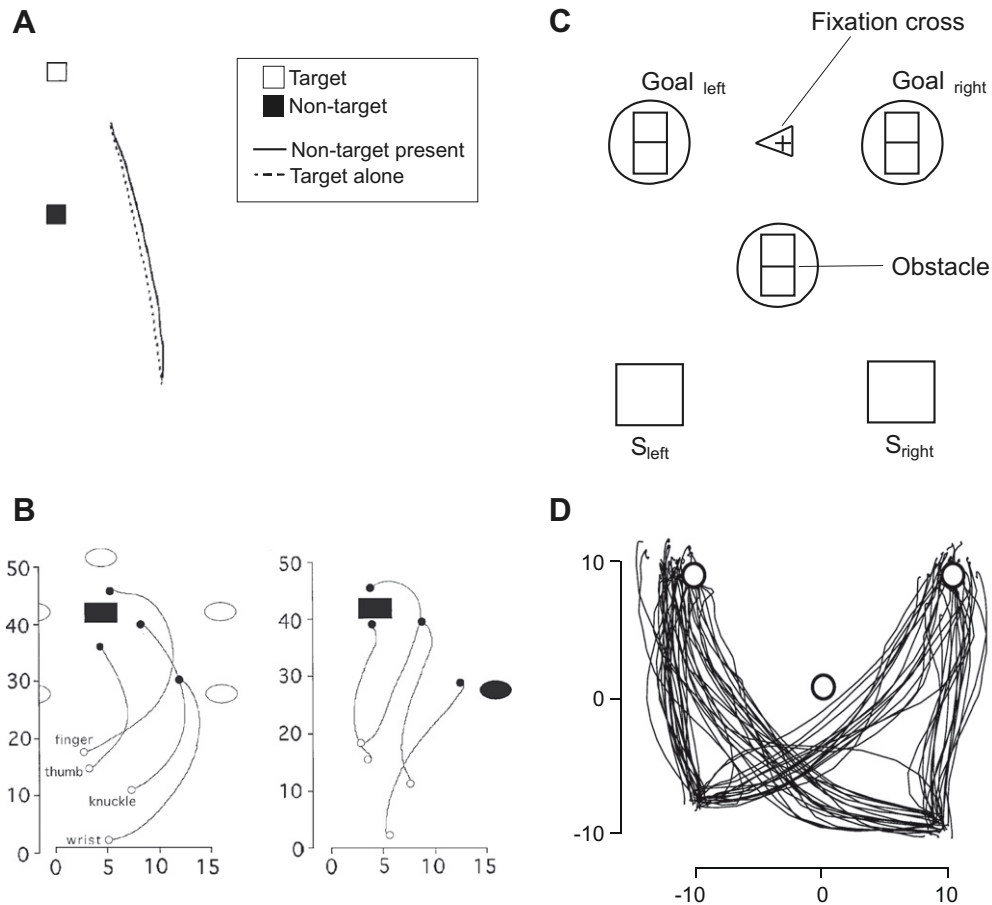


Fig. 5. Hand movement trajectories in the presence of non-targets. (A) Trajectories curve away from non-targets and visual distractors. According to Tipper et al. (1997) this is the effect of alternative, though inhibited, action plans, which are automatically afforded by the non-target stimuli (like the filled rectangle). (B) In a study by Tresilian (1998) participants had to grasp for a target object either without obstacles (left, potential obstacle positions are indicated by the unfilled ellipses) or with one obstacles present in the workspace (filled ellipse). According to Tresilian et al., obstacles constitute spatial constraints to the hand path, which have to be accounted for by keeping the hand outside a minimum distance (adapted from Tipper et al., 1997 and Tresilian, 1998). (C) Using a letter discrimination task, Deubel and Schneider (2004) analysed the deployment of visual attention to a central obstacle. Depending on the instruction to move either the right or left hand to the right or left upper goal, the central obstacle became movement-relevant or irrelevant. (D) Hand movement trajectories resulting from moving either the right or left hand around the obstacle to the right or left upper goal. The central location was only obstructive if participants had to reach along the diagonal (both adapted from Deubel & Schneider, 2004).

The behavioural significance of obstacles is also reflected in overt gaze behaviour. Obstacles are usually fixated while the hand moves around them. For example, Johansson and colleagues (2001) found that an obstacle was fixated on 80% of the trials when actors manoeuvred a bar around it. When participants were required to fixate elsewhere, the hand collided more often with the obstacle.

Deubel and Schneider (2004) measured how visual attention is covertly deployed to a central obstacle immediately before reach initialisation (see Fig. 5C). By instructing a reach with either the right or left hand towards a goal at either the right or left upper quadrant of the workspace, they manipulated on a trial-by-trial basis how task-relevant, i.e., how obstructing, a central obstacle was (see Fig. 5D). For example, the central obstacle was highly obstructive when the right hand had to reach to the upper left goal position, whereas the same obstacle was hardly relevant when the right hand had to reach to the upper right goal. The allocation of visual attention in the scene was measured by a secondary perceptual task in which the participants had to discriminate briefly presented letters that were flashed during the movement preparation at either the movement goal or at the location of the obstacle. In those trials in which the central object was obstructive, discrimination performance at the obstacle's position was significantly enhanced in comparison to trials without obstacles or trials in which the central object was not obstructive to the planned move-

ment. These results indicate a preferential processing of visual information not only at the movement goal but also at the obstacle. They suggest that an obstacle is visually attended during movement preparation if the actor is required to avoid it. So far, we do not know how the distribution of attention in the scene changes once the actor started to move or once the effector passed the obstacle.

The importance of visual attention for the successful avoidance of obstacles in reaching tasks also becomes manifest from neuropsychological studies. Not surprisingly, some patients with parietal lesions experience tremendous problems when they have to reach around or over an obstructive object. Schindler and colleagues, for example, described two patients with optic ataxia who did not exhibit normal obstacle avoidance (Schindler et al., 2004). While control participants adjusted their reaching trajectories to the variable position of two obstacles, the patients kept performing reaches along the same direct trajectory and completely ignored the obstacle configuration.

6. Parallel representation of movement goals in the primate brain

The interplay of visual attention and visual guidance of movements is reflected in the fact that both functions share common

neural structures, in humans and non-human primates. In the following we review studies that document the prominent role of a fronto-parietal network in the selection-for-action for both reach and grasp movements. Again, we will put a special focus on how these structures aid the preparation of actions that involve multiple movement goals or require the consideration of additional relevant locations. For a more comprehensive review of this network see Andersen and Cui (2009). Along the dorsal stream of visual processing, the posterior parietal cortex (PPC, Fig. 6A) has traditionally been investigated with regard to its role in the visual guidance of movements (Glickstein, 1996; Hyvärinen, 1982; Mountcastle, Lynch, Georgopoulos, Sakata, & Akuna, 1975). Monkey physiology has identified various substructures of PPC – all clustering around the intraparietal sulcus (IPS) – that encode in parallel spatial information for different effectors (Andersen & Buneo, 2002; Andersen, Snyder, Bradley, & Xing, 1997; Cui & Andersen, 2007; Konen, Kleiser, Wittsack, Bremmer, & Seitz, 2004; Rizzolatti et al., 1994; Snyder, Batista, & Andersen, 1997, 2000; see Fig. 6). The lateral inferior parietal cortex (LIP), for example, has been shown to be specifically activated during the preparation of saccadic eye movements (Colby, Duhamel, & Goldberg, 1996; Sereno, Pitzalis, & Martinez, 2001) as well as during covert shifts of attention (Chelazzi & Corbetta, 2000; Colby, 1998; Colby & Goldberg, 1999).

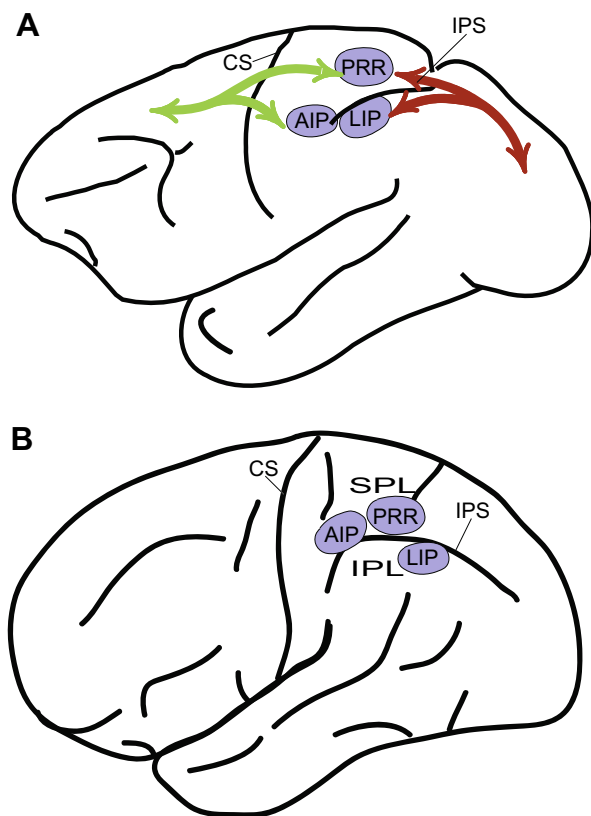


Fig. 6. The posterior parietal cortex (PPC). (A) PPC plays a crucial role in the transformation of visual input into movement plans for reaching and grasping as well as in the attentional selection of visual stimuli. Single-cell recordings in behaving non-human primates revealed a mosaic of functionally specialized areas that cluster along the intraparietal sulcus (IPS): the lateral intraparietal area (LIP) which is specifically activated before saccadic eye movements, the parietal reach region (PRR) which is selective for the planning of arm reaches, and the anterior intraparietal area (AIP) which plays a crucial role in the adjustment of hand postures for upcoming grasp movements. The arrows illustrate the bidirectional information streams to frontal motor areas (green) and to occipital areas related to visual processing (red). (B) In the human posterior parietal cortex functional imaging studies have identified homologues to the structures in monkey PPC in the inferior and superior parietal lobe (IPL, SPL).

More relevant to the preparation of hand movements, however, is the parietal reach region (PRR), which in monkeys is located along the medial bank of the IPS and area V6. Neurons in the parietal reach region were found to be specifically activated before reaching movements and have therefore been interpreted as encoding reach intentions (Buneo & Andersen, 2006; Calton, Dickinson, & Snyder, 2002; Cui & Andersen, 2007; Snyder et al., 1997; Taira, Mine, Georgopoulos, Murata, & Sakata, 1990). Neuronal circuits within PRR select goals for hand movements (Gail & Andersen, 2006; Scherberger & Andersen, 2007) and keep their representation active until the movement is executed. They also help transforming the retinal position of a target in respect to the line of gaze into other, motor-relevant frames of reference such as the directional information (Buneo, Jarvis, Batista, & Andersen, 2002), as represented in frontal motor structures that finally guide the hand to the goal. Neuroimaging studies in humans found a possible homologue of PRR in the human intraparietal sulcus (see Fig. 6B; Connolly, Goodale, Desouza, Menon, & Vilis, 2000; DeSouza et al., 2000; Kertzman, Schwarz, Zeffiro, & Hallett, 1997; for a detailed review of the cognitive functions of human PPC see Culham & Kanwisher, 2001).

Binkofski et al. (1999a, 1999b) showed in humans that a more anterior area within the posterior parietal cortex, the anterior intraparietal area (AIP, see Fig. 6B), is typically activated during visually guided grasping (see also Castiello, 2005; Culham, 2003; Culham & Valyear, 2006; Culham et al., 2003; Shikata et al., 2003, 2008). In further functional imaging studies this patch of human cortex turned out to be sensitive also to the mere presentation of graspable objects (Chao & Martin, 2000). Tunik, Frey, and Grafton (2005) further fostered the view that the anterior intraparietal area (AIP) is involved in the pre-shaping of the grasping hand. When they applied transcranial magnetic stimulation (TMS) to the anterior part of intraparietal sulcus the participants were no longer able to accurately adjust the hand posture to sudden changes in the orientation of the to-be-grasped object. This effect of the magnetic stimulation was restricted to AIP, while stimulation at other parietal sites did not hamper grasping movements (similar to Glover, Miall, & Rushworth, 2005). The anterior part of PPC therefore seems crucial for the preparation of points of grasping application. In humans, lesions to the PPC often cause disorders also in the planning and execution of simpler, goal-directed hand movements, such as reaching or pointing, e.g. in limb apraxia and optic ataxia (see Balint, 1909). Lesions that cause optic ataxia in humans almost always include the intraparietal sulcus (IPS) and sometimes involve parts of the inferior or superior PPC (Culham & Valyear, 2006). Karnath and Perenin (2005) compared many case studies of optic ataxia and found the IPS and adjacent regions to be commonly involved in these deficits. Taken together, several structures along the intraparietal sulcus subserve the programming of various manual actions. For this the PPC is reciprocally connected with many frontal planning- and motor-related structures (especially with premotor areas, see Pesaran, Nelson, & Andersen, 2008).

Most importantly, however, there is also the second prominent function of PPC: it is widely agreed that the posterior regions of the parietal cortex play a crucial role in shifting spatial attention. In human and non-human primates, attention-related activity has been found throughout PPC at the level of single cells (e.g., Bisley & Goldberg, 2003; Colby & Goldberg, 1999; Corbetta & Shulman, 2002; Rushworth, Paus, & Sipila, 2001) as well as at the level of metabolic activity of whole brain areas (see, e.g., Corbetta, Kincade, Ollinger, McAvo, & Shulman, 2000; Corbetta, Miezin, Shulman, & Petersen, 1993; Corbetta et al., 1998; Giesbrecht, Woldorff, Song, & Mangun, 2003; Perry & Zeki, 2000; Wojciliuk & Kanwisher, 1999; Yantis et al., 2002). Shikata et al. (2003) found an increased BOLD signal in the anterior IPS (a proposed homologue to non-hu-

man AIP) when they compared a pure attentional task, namely the visual discrimination of surface orientations, with the imagination

of a grasping movement as well as with the actual execution of a grasp movement. This gradually increasing activity mirrors the

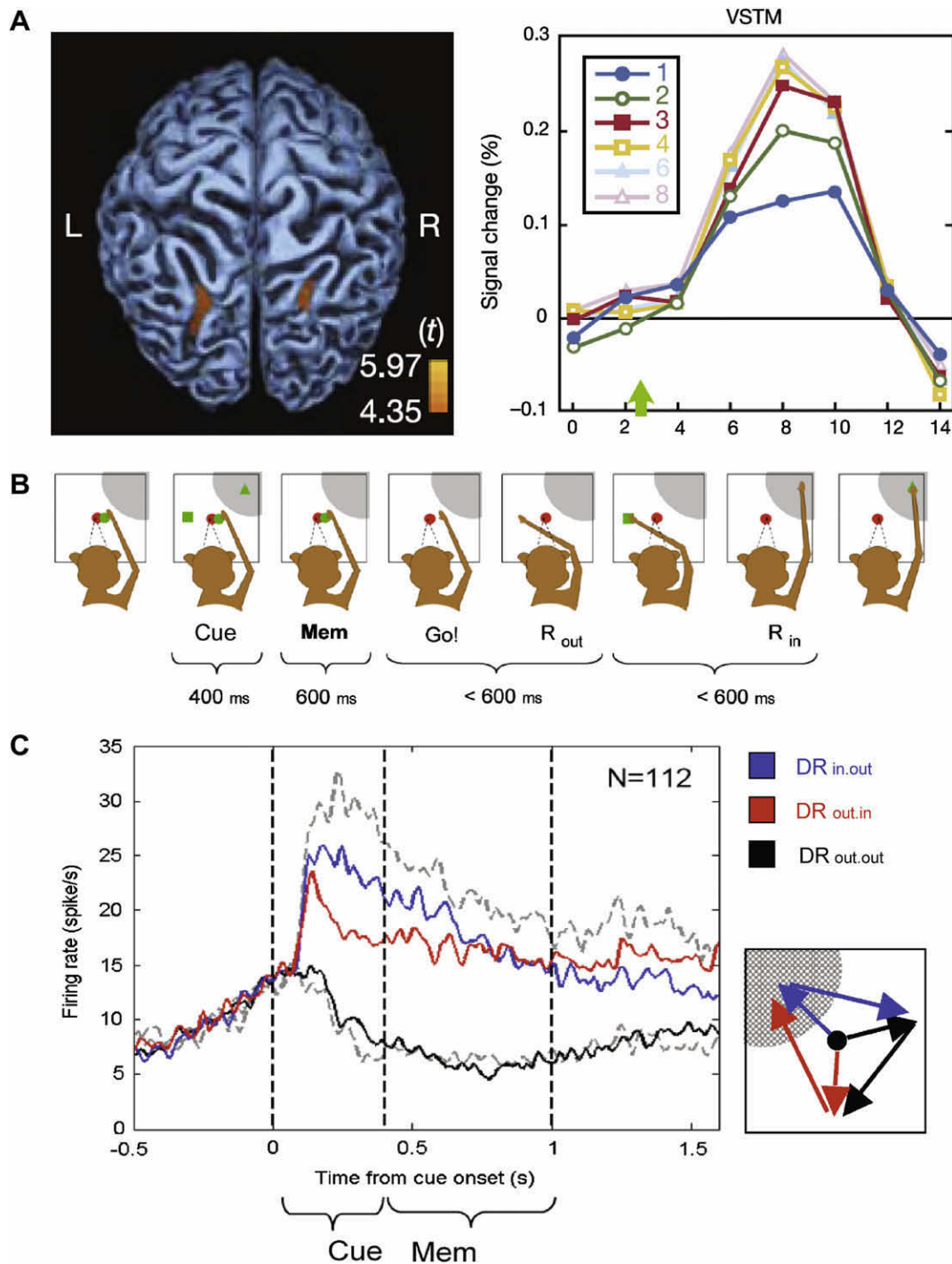


Fig. 7. (A) The activity in the posterior parietal cortex reflects the load of the visual working memory. Activation of posterior parietal cortex increases with the number of items to be remembered in a memory task (adapted from Todd & Marois, 2004). (B) Sequential double-reach task used by Baldauf et al. (2008). Each panel depicts the monkey sitting in front of the touch-screen. Labels of the task epochs and their durations are below the panels. The grey areas indicate the response field of an example cell. Central eye fixation at the central red dot was required and monitored during the whole trial. At the beginning of each trial the monkey positioned his hand at the central green circle. During the cue period, a first and second reach goal was simultaneously cued for 400 ms by a green square and triangle, respectively. After the cues were extinguished, the monkey had to memorize both locations for 600 ms (memory period, 'Mem'). After the memory period, the central green circle disappeared (GO-signal, 'Go!'). The monkey then had to reach first to the location in which the square had been presented and then to the location in which the triangle had been shown. Both reaches had to be performed in a rapid sequence, within 600 ms each. Once a position was reached with sufficient accuracy, the original cue stimulus flashed again for 100 ms providing the monkey with visual feedback in the periphery. Single unit activity was analysed during the memory period that ensued after the cue offset as a function of whether the first or second movement goal was inside the cell's response field. (C) Average firing rate of the recorded parietal population in three experimental conditions: Double-reaches with only the first goal inside the cell's response field are shown in blue ('DR_{in.out}'), reach sequences with only the second reach goal inside the response field are shown in red ('DR_{out.in}'). The black trace represents the baseline activity if no reach goal was inside the response field ('DR_{out.out}'). During the memory period (0.4–1.0 s after cue onset) most PRR neurons prospectively represented the first (blue) and second movement goal (red) to about the same extent (adapted from Baldauf et al., 2008).

similarity between action preparation and perceptual tasks with respect to the attentional demands. The double function of the PPC shows how perceptual attention and action preparation are potentially linked in terms of neural substrates.

But, importantly for the scope of this review, does the parietal cortex also represent multiple activation foci, e.g., when more complex movement tasks are involved? Frontal planning areas are well documented to do so whether various goals are planned to be reached in sequence (e.g., Averbach, Sohn, & Lee, 2006; Lu & Ashe, 2005; Tanji & Shima, 1994) or oppose each other as alternative plans during decision forming (Cisek, 2006; Cisek & Kalaska, 2005). We indeed believe that a crucial aspect of the normal function of parietal cortex is to maintain multiple attentional foci. Barash (1996) pointed out that the neuropsychological syndrome of extinction gives a strong hint to the involvement of the parietal cortex in the representation of multiple areas of interest. Patients who suffer from extinction after lesions to the PPC are unable to detect two stimuli presented simultaneously in the left and right hemifield. Milner (1996) therefore described extinction as a pathological attentional bias to the ipsi-lesional field (in the sense of a biased competition model, see Desimone & Duncan, 1995). This suggests that the PPC in healthy humans is essential for the processing of two simultaneous stimuli. As mentioned before, Schindler and colleagues (2004) reported cases in which damage to the PPC caused patients to ignore additionally placed object configurations that were known to automatically affect the movement trajectories in healthy controls. Courtney, Ungerleider, Keil, and Haxby (1996) showed in a PET study that the superior parietal lobe (SPL) was bilaterally activated by a working memory task in which participants had to remember three locations in the visual field. Todd and Marois (2004) used functional MRI and showed that activity in PPC correlates with the amount of spatial information that is stored in the visual short-term memory (see Fig. 7A). Culham and colleagues previously showed similar gradual increases of parietal BOLD responses by parametrically varying the attentional load in a multiple-object-tracking task (Culham, Cavanagh, & Kanwisher, 2001). Therefore, PPC has the capacity to simultaneously represent multiple locations in space.

Recently, Baldauf et al. (2008) recorded from single neurons in monkey's parietal reach region while the animals were preparing for a double-reach task to two peripheral goal locations (Fig. 7B). After mapping the response fields of single units in PRR they placed either the first or the second goal of a reach sequence in the response field of a cell. When analysing the neuronal activity during a memory-period, which was between the presentation of the movement cues and the go-signal, they could attribute the cell's planning activity to the representation of either the first or second goal position. Most of the cells within PRR encoded immediate goals and subsequent goals equally well (Fig. 7C). This implies that the parietal reach region encodes multiple movement goals of a planned hand movement sequence in parallel. With regard to the dynamics of the representation of the first and second movement goal the authors showed that both goal representations were simultaneously activated from the very beginning of the memory period. After completion of every sequence component, the respective neural representation soon receded to baseline activity. Given that the parietal reach region has a roughly retinotopic organization (Swisher, Halko, Merabet, McMains, & Somers, 2007), the eye-centred planning activity in PRR has been argued to be a likely source of attentional top-down signals that facilitate visual processing at multiple goal positions.

Functionally, the output of neural populations in PPC could be projected bi-directionally: the encoding of movement intention could be passed to further motor-related structures in the frontal brain, whereas the very same output could also be back-projected (top-down) to early visual areas and subserve attentional "selec-

tion-for-action". The reach- and grasp-related structures within the posterior parietal cortex "seem to do double duty" (Milner, 1996) and may mediate the interconnection of both functions in the sense of the premotor theory of attention (Rizzolatti et al., 1994).

7. Conclusions and future directions

We have reviewed several lines of research about the relationship of spatial attention and movement preparation. First, studies in which observers prepare a movement sequence to two or three targets have revealed that attention during planning spreads to all action-relevant movement goals. This occurs temporally in parallel, with the amount of perceptual enhancement reflecting the serial order of the required movements. Second, when observers plan to grasp an object, experimental results have demonstrated that perceptual resources are biased towards all those locations on the object that will be grasped. Third, evidence from behavioural studies has demonstrated that a potential obstacle and the movement target are both attended during movement planning. Finally, recent neurophysiological studies point to a parallel representation of several action-relevant locations in the posterior parietal cortex.

Taken together, the studies provide compelling evidence for the assumption that the planning of a complex movement enacts the formation of an "attentional landscape" which tags all those locations in the visual lay-out that are relevant for the impending action. Obviously, this landscape is more complex than a simple "spotlight" or a "gradient" model of attention in that it specifically tags all those locations in the visual lay-out that are relevant for the impending action. Despite the basically serial nature of movement generation, the findings imply a concurrent deployment of attentional resources to multiple locations, rather than the sequential processing of the action-relevant locations and features by a serial mechanism. Additionally, the studies show that more attentional resources are dedicated to the location of the immediately following movement goal, and to those parts that require more precise motor control. Thus, it seems that more than just selecting the action-relevant locations, the distribution of attentional weights also mirrors further, motor-related aspects such as temporal instancy, required accuracy, and the difficulty of the future action.

We focused our review on the attentional landscape that is found *before* the onset of the overt action. However, this attentional map is certainly dynamic and changes during the course of movement preparation, execution and correction. Therefore, we think it will be of considerable importance for the understanding of motor actions to study also, in future investigations, the deployment of covert attention during the execution and on-line correction of the movements, and possibly even during the subsequent manipulation of the target objects. We expect that multiple foci of attention will also become evident in these later phases, and that these will provide information on which parts and features of the movement goals and the visual context are continuously integrated into the action flow.

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