Theory of Visual Attention (TVA) in Action: Assessing Premotor Attention in Simultaneous Eye-Hand Movements

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Word count:

Author Note: The data will be made available on the Open Science Framework.

Conflict of interest: The authors declare no conflicts of interest.

Acknowledgements: The authors thank Kathrin Finke, Marleen Haupt, Natan Napiórkowski, and members of the Deubel laboratory for helpful advices and discussions.

Funding: This work was supported by the Deutsche Forschungsgemeinschaft (DFG), grant DE336/5-1.

Author Contributions: All authors developed the study concept and contributed to the study design. P.K. and N.M.H. collected and analyzed the Data. All authors interpreted the data. P.K. drafted the manuscript, and H.D. and N.M.H. provided critical revisions. All authors approved the final version of the manuscript for submission.

Running title: Premotor attention in simultaneous eye-hand movements

Abstract

Attention shifts that precede goal-directed eye and hand movements are regarded as markers of motor target selection. Recent studies found parallel allocation of visuospatial attention to saccade and reach targets during simultaneous eye-hand movements, arguing in favor of independent, effector-specific target selection mechanisms. This raises the question whether the overall attention capacity increases with the number of active effectors. In a modified Theory of Visual Attention (TVA; Bundesen, 1990) paradigm, participants reported briefly presented letters during eye, hand, or combined eye-hand movement preparation to centrally cued locations. Modeling the data according to the TVA allowed us to assess both the overall attention capacity as well as the deployment of visual attention to individual locations in the visual work space. In two experiments, we show that attention was predominantly allocated to the motor targets – without competition between effectors. The parallel benefits at eye and hand targets, however, had concomitant costs at non-motor locations, and the overall attention capacity was not increased by the simultaneous recruitment of both effector systems. Moreover, premotor shifts of attention dominated over voluntary deployment of processing resources, yielding severe impairments of voluntary attention allocation. We conclude that attention shifts to multiple effector targets without mutual competition, given that sufficient processing resources can be withdrawn from movement-irrelevant locations.

Keywords: Selective Attention, Theory of Visual Attention, Hand Movements, Saccades

Introduction

When briefly confronted with multiple visual objects in a display, only a subset of the information can be processed due to limited capacities of the visual system. Attention allows the selection of the currently most relevant information in order to guide our behavior adequately (Carrasco, 2011). Based on the biased competition principle (Desimone & Duncan, 1995), the Theory of Visual Attention (TVA; Bundesen, 1990) provides a mathematical description of parallel processing of visual objects which compete for selection into visual short-term memory (vSTM). The model accounts for various findings from behavioral and neurophysiological studies on selective attention (Bundesen & Habekost, 2014). According to the TVA, the rate ($v(x,i)$) at which an object is categorized and competes to be successfully encoded into vSTM is described by three terms: the sensory strength ($\eta(x,i)$) of an object *x* belonging to the category *i*, the perceptual bias (β_i) associated with the category, and the relative attentional weight associated with the object (w_x):

$$v(x,i) = \eta(x,i)\beta_i \frac{w_x}{\sum_{z \in S} w_z}. \quad (1)$$

Importantly, attentional weights are derived from pertinence values and bias the selection of objects for successful categorization and short-term storage (Bundesen & Habekost, 2014). The TVA has been successfully applied to determine age-related changes in attention selectivity and capacity across the lifespan (McAvinue et al., 2012), to assess cognitive impairments in several patient groups (Bublak et al., 2005; Duncan et al., 1999; for a review, see Habekost, 2015), and to measure different components of visual attention in healthy controls (Finke et al., 2005). Yet, the TVA-based assessment of visual attention has only been studied under fixation, taking no account of attention mechanisms in relation to selection-for-action (Allport, 1987). Despite the well-established finding that both saccades (Deubel & Schneider, 1996; Kowler, Anderson, Dosher, & Blaser, 1995; Montagnini & Castet, 2007) and hand movements (Baldauf, Wolf, & Deubel, 2006; Deubel, Schneider, & Paprotta, 1998; Rolfs, Lawrence, & Carrasco, 2013) are preceded by obligatory shifts of visual attention towards their motor targets, it is unclear how action-coupled attention shifts modify the selection of competing objects for successful encoding into vSTM. To approach this question, we combined a TVA paradigm with eye-hand movement tasks to

investigate how motor preparation affects the deployment of visual attention over multi-element displays. To our knowledge, this is the first study to assess premotor shifts of visual attention via the TVA framework, which offers a key advantage over conventional approaches to measure premotor attention: The TVA allows the assessment of both the overall attention capacity (parameter *C*) and the allocation of attentional resources to individual objects (parameter *v*) in a display. We reasoned that our novel TVA paradigm allowed us to address a controversially debated research question concerning the distribution of attention prior to combined eye-hand movements. Looking and reaching simultaneously to spatially separate goals requires the selection of multiple movement targets. Research on whether motor targets of different effectors are selected by a single system or by independent, effector-specific systems has yielded conflicting results. Support for a unitary selection mechanism came from behavioral studies investigating the deployment of visual attention – an index of movement target selection – during the preparation (Khan, Song, & McPeek, 2011; Neggers & Bekkering, 2000) or execution (Nissens & Fiehler, 2018) of combined eye-hand movements. These studies reported attentional competition between eye and hand target selection, i.e. the deployment of attention to one effector target was affected by the motor preparation of the other effector. Other studies, in contrast, observed increased attention deployment at both eye and hand target locations without any trade-off (Hanning, Aagten-Murphy, & Deubel, 2018; Jonikaitis & Deubel, 2011). These studies showed that during the preparation of simultaneous eye-hand movements, attention rises in parallel at both motor targets, indicating that attention can be allocated towards both effector targets independently and without impairments arising from the necessity to plan two movements versus a single movement (see Hanning et al., 2018, for a discussion of the diverging results).

On the one hand, such parallel allocation of attention to multiple effector targets without competition can be explained by separate attentional resources dedicated to each individual effector. On the other hand, it may also be explained by a withdrawal of attentional resources from non-motor locations. To shed light on this controversy, we combined a classical TVA whole report paradigm with eye-hand movement tasks. In a first experiment, we assessed whether the parallel

preparation of eye and hand movements to spatially separate goals enhances visual processing at both effector targets simultaneously and independently of each other, and whether such parallel processing benefits would be reflected in increased overall attention capacity. In experiment 2, we investigated whether attention was withdrawn from non-motor locations in order to allocate processing resources towards the motor targets and whether these costs occurred obligatorily. We used a similar paradigm as in experiment 1. In addition to the perceptual and motor task, we gave participants an incentive to voluntarily deploy their attention primarily to a subset of the presented items: different colors (50% red and 50% blue) indicated whether the letters were associated with a high or low monetary reward. This allowed us to investigate the ability to voluntarily deploy attention while performing eye-hand movement tasks.

Altogether, our experimental design allows us to (a) determine whether attention is deployed to the eye and hand targets in parallel, (b) whether such parallel allocation leads to an increase in the overall attention capacity or is associated with concomitant costs at non-motor locations, and (c) how our goal-directed actions influence our ability to voluntarily attend elsewhere.

Experiment 1

In this experiment, we established the TVA framework as a sensitive tool to measure action-related shifts of visual attention. First, we examined if attention is deployed in parallel to eye and hand movement targets and whether effectors compete for attentional resources. Second, to test the hypothesis of independent, effector-specific target selection mechanisms, we measured whether the overall attention capacity increases with the number of active effectors.

Methods

Participants. Eight healthy human adults (age range: 24-31 years, four female, one left-handed) participated in the experiment (including authors PK and NMH). All participants had normal or corrected-to-normal visual acuity. We determined our sample size based on previous research on

premotor shifts of visuospatial attention using between five and nine participants (e.g., Hanning et al., 2018; Khan et al., 2011). The experimental protocols were approved by the local ethical review board of the Faculty of Psychology and Education of the Ludwig-Maximilian-University Munich and in accordance with the Declaration of Helsinki. Participants gave written informed consent and were compensated at the rate of €10/hr.

Apparatus. Participants performed the task in a dimly illuminated laboratory, viewing the stimuli binocularly on a 32-inch, 25°-inclined LCD touch display (Elo 3202L Interactive Digital Signage, Elo Touchsystems, Menlo Park, CA, USA) with a refresh rate of 60 Hz and a spatial resolution of 1,920 × 1,080 pixels. The viewing distance to the screen midpoint was 50 cm. An EyeLink 1000 Tower Mount (SR Research, Osgoode, Ontario, Canada) video-based eye tracker recorded the gaze position of participants' dominant eye at a sampling rate of 1 kHz. To minimize head movements during the task, participants' heads were stabilized by a combined chin and forehead rest (see fig. 1a). The experiment was programmed in Matlab (MathWorks, Natick, MA, USA), using the Psychophysics (version 3.0.14; Kleiner et al., 2007) and EyeLink toolboxes (Cornelissen, Peters, & Palmer, 2002). Stimulus display and data collection were controlled by a display personal computer (graphics card: NVIDIA GeForce GTX 1070), connected to the eye tracker's host computer.

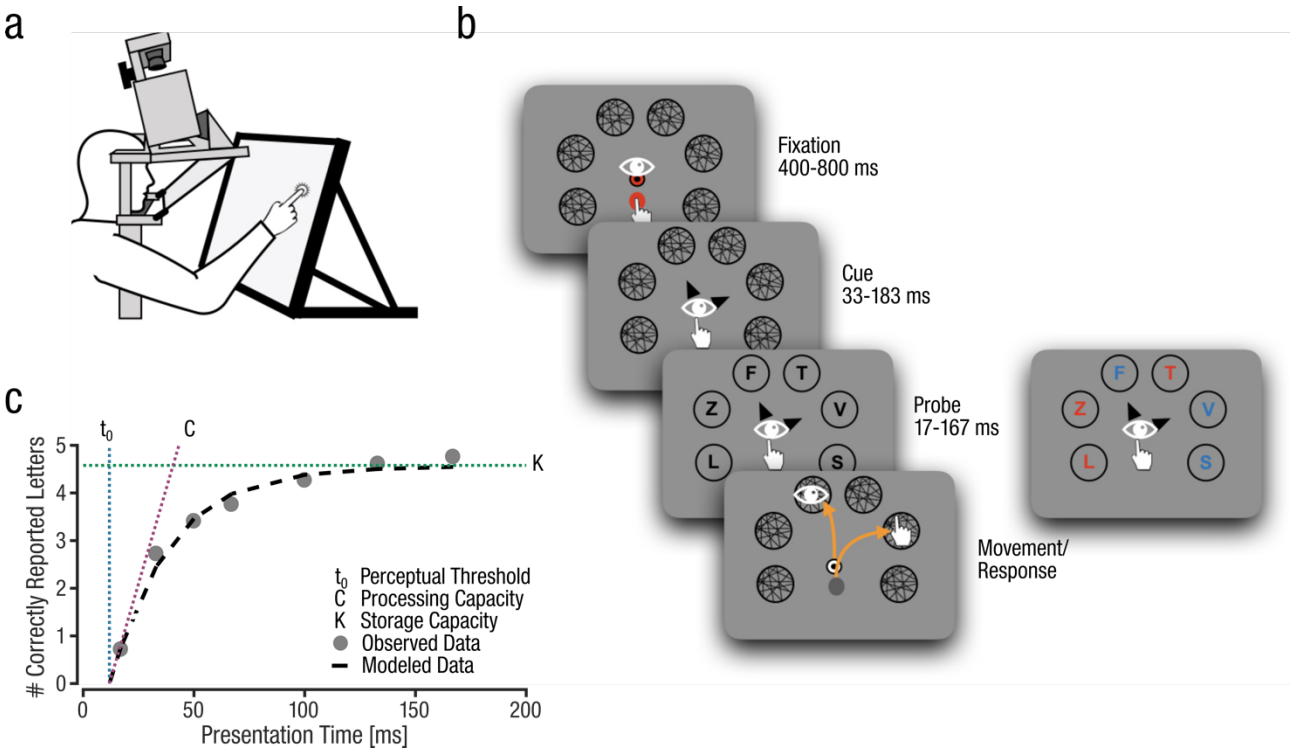

Figure 1. (a) Experimental setup. Participants' head was fixated on a forehead and chin rest, gaze position of the dominant eye was tracked with an eye-tracker and hand movements of the dominant right hand were recorded by a touch screen. **(b)** Trial sequence. Six circularly arranged masking stimuli appeared. Following a fixation period, two central arrow cues indicated the potential motor targets. Depending on the experimental condition, participants either kept fixating or prepared an eye and/or hand movement toward the indicated target locations. After a random delay, six letters were presented for a varied duration, which participants had to report at the end of the trial. In Experiment 1, letters and masks were black. In Experiment 2, letters and masks were colored in red and blue. **(c)** Example TVA fitting curve (black line). Grey dots depict the observed data points averaged across presentation times. The intersection of the fitting curve with the x-axis defines the perceptual threshold (t_0), the initial slope at t_0 is defined as the processing capacity (*C*), and the asymptote of the curve defines the storage capacity of vSTM (*K*).

Stimuli and Procedure. In order to examine the overall attention capacity and the allocation of attention to motor and non-motor targets, we used a TVA whole report paradigm and measured the categorization performance of letter stimuli presented at six spatially fixed locations while varying the presentation time (17-167ms) between trials. In a randomized block design, participants were instructed at the beginning of each block to either fixate in the center (*FIXATION*), to perform single eye or hand movements (*EYE* or *HAND*), or to perform simultaneous eye and hand movements (*EYE-HAND*). **Figure 1b** depicts the trial sequence. At the

beginning of each trial, participants fixated a black-and-white bull's eye (0.5° visual angle) presented on a uniform grey background (28.2 cd/m^2) and placed their right index finger on a dark grey oval (0.6° × 0.65°) below the bull's eye. Six black circles (2° radius), arranged along a 8° virtual semicircle (evenly spaced between 70° and 290°) marked the stimulus locations. The trial started once stable eye and finger fixation was detected within a 2.25° radius virtual circle centered on the fixation targets. Six dynamic circular pre-masks composed of randomly oriented black lines were presented at the stimulus locations, which had a random orientation that changed at a rate of 30 Hz. 400 - 800 ms after pre-mask onset, two black arrow cues (0.25° × 0.5°) were presented around the bull's eye (with a distance of 1.5°) pointing to two of the six stimulus locations, randomly selected. In the *FIXATION* condition, participants were instructed to ignore these cues. In the single movement conditions (*EYE* or *HAND*), participants chose one of the two locations and moved the respective effector (eye or hand) to the selected location as fast and as precisely as possible, while the other effector remained at fixation. In the *EYE-HAND* condition, participants moved each effector to one of the cued locations, at free choice. Note that we always presented two cues irrespective of the experimental condition to keep the visual input constant. This way a potential difference in overall attention capacity cannot be explained by visual bottom-up processes. Following a stimulus onset asynchrony (SOA) of 33.3 - 183.3 ms after cue onset, the pre-mask was replaced by six letters, selected from a subset of 19 letters (ABEFHJKLMNPRSTVWXYZ). The letters were presented for a duration of either 17, 33, 50, 67, 100, 133, or 167 ms. SOA and letter presentation duration were matched such that the letter presentation always ended 200 ms after cue onset, i.e. within the movement latency. Subsequently, the dynamic masks reappeared and were presented for another 800 ms. Afterwards, participants verbally reported all letters they had perceived and received online feedback if the motor task was not correctly performed.

Participants performed at least 16 experimental blocks (four of each experimental condition) of at least 70 trials each. We controlled online for broken eye and finger fixation (outside 2.25° from fixation), too short (<170 ms) or too long (>700 ms) movement latencies, and incorrect eye or hand

movements (not landing within 2.25° from the indicated targets). Erroneous trials were repeated in random order at the end of each block. If motor performance was incorrect in more than 50% of trials within a block, the whole block was excluded and repeated (this was the case for two blocks for one participant). Overall, participants moved their eyes and hand incorrectly to the same target in 5.2% ± 0.28 (mean ± SE) %, made eye movement errors in 13.5 ± 0.78 % (broken fixation: 6.0 ± 0.52 %, incorrect saccade: 7.5 ± 0.37 %) and hand movement errors in 2.0 ± 0.19 % (broken fixation: 0.22 ± 0.03 %, incorrect hand movement: 1.8 ± 0.17 %) of trials.

Data Analysis. Data was analyzed offline using custom-made routines in Matlab (MathWorks, Natick, MA, USA). We measured eye and finger position in x- and y-screen-centered coordinates and determined saccade and reach movement onset, landing time, and position. Saccades were detected based on the eye velocity profiles of the recorded eye (Engbert & Mergenthaler, 2006). Saccade and hand movement latencies were defined in relation to motor cue onset. Offline criteria for correct trials were as follows: (1) eye and hand maintained fixation within a 3° radius centered around the effector's fixation position until cue onset, and the passive effector(s) in the *EYE*, *HAND*, or *FIXATION* conditions maintained fixation until the end of the trial, (2) eye and hand movements landed no further than 3° from motor targets center and stayed there for at least 50 ms, and (3) no blinks occurred during the entire trial. Based on these criteria, 8.72% of all online accepted trials were discarded.

We modeled the remaining trials according to the TVA in two steps. First, we implemented TVA modeling procedures using the libTVA toolbox for Matlab (Dyrholm, Kyllingsbæk, Espeseth, & Bundesen, 2011), in order to measure the allocation of attention to individual stimulus locations. To this end, we used the location-specific estimation of the processing rates (v) but rearranged the data in order to estimate v-values for motor versus non-motor targets. Perceptual thresholds (t_0) – the minimum presentation time at which an observer performs better than chance – were estimated for each participant and experimental condition but were assumed to be constant for the different target types within an experimental condition. The observed and estimated values for

cued and uncued locations were averaged to obtain single measures for the non-motor locations. Second, we assessed the influence of movement preparation on the deployment of visual attention over the whole stimulus display. For this, the following standard TVA parameters were extracted separately for each participant and experimental condition: (1) t_0 (perceptual threshold), (2) K (visual short-term memory capacity) – the maximum number of items an observer can remember and report, and (3) C (processing capacity) – the summed processing rates (v) of all items in the visual work space (for exemplary fitting curves and the extracted parameters, see **fig. 1c**). For all analyses, t_0 was set to 0 ms if its estimation was < 0 ms.

To evaluate the differences in overall attention parameters across experimental conditions, as well as differences in attention deployment within each condition, we ran multiple repeated-measures analyses of variance (rmANOVA). Sphericity was assessed using Mauchly's test and Greenhouse-Geisser-corrected *p*-values are reported in case of significance. An alpha level of 0.05 was chosen and *p*-values were Bonferroni-corrected for post-hoc pairwise comparisons. All statistical analyses were performed in RStudio version 1.0.136 (RStudio, Boston, MA, USA).

Results

The first aim of the current study was to assess how action-coupled shifts of visual attention modify the selection of competing objects for successful encoding into visual short-term memory (vSTM). In particular, we were interested in whether the parallel preparation of eye and hand movements enhances attentional processing at both effector targets simultaneously and independently of each other, and whether such parallel processing benefits are reflected in the overall attention capacity, i.e. whether attention capacity increases with the number of active effectors.

Allocation of Attention at Motor Targets versus Non-Target Locations. We expected increased allocation of attention at the motor targets in the single movement conditions (*EYE* and *HAND*). Moreover, based on previous studies finding parallel allocation of attention in

simultaneous eye-hand movements (Hanning et al., 2018; Jonikaitis & Deubel, 2011), we expected attention to be equally deployed to both the saccade and the reach target in the *EYE-HAND* condition.

To test these hypotheses, we estimated the processing rates (v) of items presented at motor targets versus non-targets (for fitted curves of a single subject, see **fig. 2a**). **Figure 2b** shows the extracted v-parameters for the different target types in each experimental condition averaged across all participants. For the *FIXATION* condition, a paired t-test between averaged processing rates at cued and uncued locations revealed no significant difference ($p = 0.067$). For the other experimental conditions, we ran separate one-way rmANOVAs with factor *target type*, revealing significant effects in each effector condition between motor targets, cued but not selected locations and uncued locations (*EYE*: $F(2,14) = 29.61$; $p = 0.001$; $\eta_p^2 = 0.809$, *HAND:* $F(2,14) = 47.76$; $p < 0.001$; $\eta_p^2 = 0.872$, and *EYE-HAND*: $F(2,14) = 17.78$; $p < 0.001$; $\eta_p^2 = 0.718$). Post-hoc, pairwise comparisons indicated a similar deployment of attentional resources in both single movement conditions: processing rates were increased at the motor targets compared to the averaged processing rates at the uncued locations ($t(7) = -5.52$; $p = 0.003$; 95% CI [-51.02, -20.43] and $t(7) = -7.88$; $p < 0.001$; 95% CI [-28.60, -15.40] for *EYE* and *HAND*, respectively) and at the second cued but not selected location (*EYE* : $t(7) = -5.40$; $p = 0.003$; 95% CI [-43.51, -16.98] and *HAND*: $t(7) = -6.82$; $p = 0.001$; 95% CI [-21.72, -10.54]). Contrary to the *FIXATION* condition, in both single movement conditions, we furthermore observed significant differences between the cued (but not selected) and the uncued locations (*EYE*: $t(7) = -4.21$; $p = 0.012$; 95% CI [-8.56, -2.41] and HAND: $t(7) = -3.43$; $p = 0.033$; 95% CI [-9.91, -1.83]), suggesting that the central cues only modulated performance once they indicated potential movement targets. In the *EYE-HAND* condition, we compared the processing rates between the motor targets and the averaged processing rates at non-targets, as well as between the two effector targets. Processing rates were strongly increased at both the saccade ($t(7) = -4.76$; $p = 0.006$; 95% CI [-35.26, -11.86]) and reach target ($t(7) = -7.40$; $p < 0.001$; 95% CI [-20.94, -10.80]), compared to the non-targets. Importantly, no difference was

observed between the eye and hand targets ($p = 0.378$), indicating that there was no dominance of one effector over the other.

Taken together, these results demonstrate that during eye and hand movement preparation, processing resources are preferably allocated towards the motor target(s): in all movement conditions the processing rate was enhanced at eye and hand targets compared to both the uncued locations as well as to cued but not selected locations. This suggests that the processing benefit at the motor targets is caused by the coupling between visual attention and eye and hand target selection and cannot be explained by the mere presence of visual cues. Importantly, and in line with our hypothesis, when eye and hand movements are prepared simultaneously, we found enhanced performance at both the eye and the hand target, without any trade-off between the two effectors.

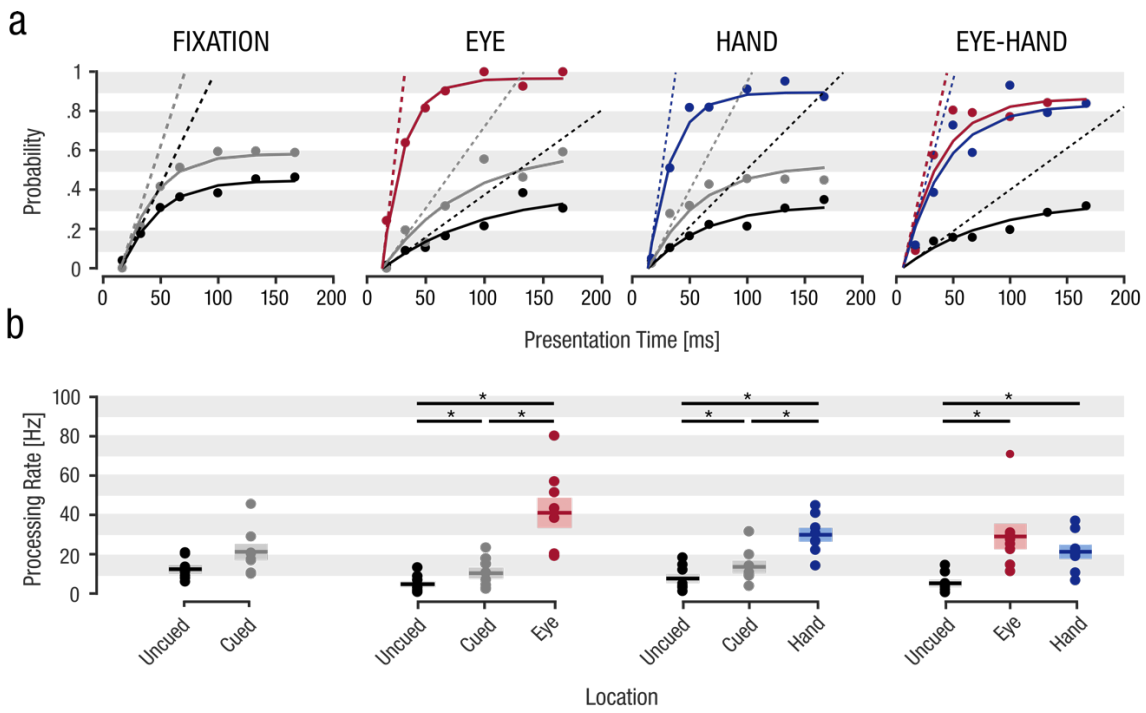

Figure 2. Encoding probability and speed at motor targets and non-targets in Experiment 1. **(a)** Encoding probability of a representative observer at the different locations as a function of letter presentation duration, separately for each experimental condition. Dots depict observed data points averaged per target type (e.g. across all uncued locations) and presentation duration, solid lines represent the fitting curves for each target type in the different experimental conditions. Dashed lines represent the extracted processing rates (v). **(b)** Extracted v-parameter averaged across all participants for the respective locations and experimental conditions. Dots depict

individual data points, horizontal lines represent the sample mean, and shaded areas visualize ± 1 standard error of the mean (SEM). Asterisks represent significant *p*-values < 0.05.

Attention Capacity Across the Whole Stimulus Display. The simultaneous enhancement of visual processing at two separate locations – the eye and the hand target – may be associated with an overall enhancement in attention capacity over the whole visual work space; i.e., the processing rate of items into visual short-term memory (vSTM) may increase with the number of active effectors. This would be in line with the assumption of independent, effector-specific attentional mechanisms. Alternatively, the parallel processing benefits at eye and hand targets may have concomitant costs at other, movement-irrelevant locations, such that the overall attention capacity would be independent of the number of recruited effectors. To distinguish between these two possibilities, we evaluated the overall attention capacity by modeling the item classification rate over the whole stimulus display (**fig. 1c**) and extracted the TVA parameters for each experimental condition (**fig. 3**). A one-way rmANOVA with factor *experimental condition* revealed no main effect on the perceptual threshold ($p = 0.186$) but on processing capacity ($F(3,21) = 6.61$; $p = 0.002$; $\eta_p^2 = .486$) and vSTM storage capacity ($F(3,21) = 9.92$; $p = 0.006$; $\eta_p^2 = .586$). Contrary to the hypothesis of attention capacity increasing with the number of active effectors, pairwise post-hoc comparisons revealed a slight decrease for both processing capacity and vSTM storage capacity between the *FIXATION* and the movement conditions: between the *FIXATION* and *EYE* condition we observed a significant decrease of the processing capacity (*C*) ($t(7) = 6.51$; $p = 0.002$; 95% CI [26.19, 56.09]; all other comparisons $p > 0.077$). For vSTM storage capacity, post-hoc comparisons revealed significant differences between the *FIXATION* and all movement conditions ($t(7) = 4.09$; $p = 0.03$; 95% CI [0.15, 0.55], $t(7) = 6.22$; $p = 0.002$; 95% CI [0.24, 0.54], and $t(7) = 5.36$; $p = 0.006$; 95% CI [0.24, 0.62], for comparisons between the *FIXATION* condition and the *EYE*, *HAND*, and *EYE-HAND* condition, respectively). Thus, overall attention capacity did not rise with the number of active effectors, but rather was slightly reduced in the single and combined movement conditions compared to the *FIXATION* condition. This may be explained by the increased workload in the movement conditions: Instead of focusing exclusively

on the letter identification task, in the movement conditions also the arrow cues had to be interpreted and the corresponding actions to be performed.

In sum, we demonstrated that attention is primarily allocated towards effector targets, increasing their probability to be encoded into vSTM. When eye and hand movements are programmed simultaneously, processing resources are similarly increased at both locations and without one effector dominating the other. Moreover, we showed that the overall attention capacity is constant, suggesting that attentional costs should occur at other, non-target locations.

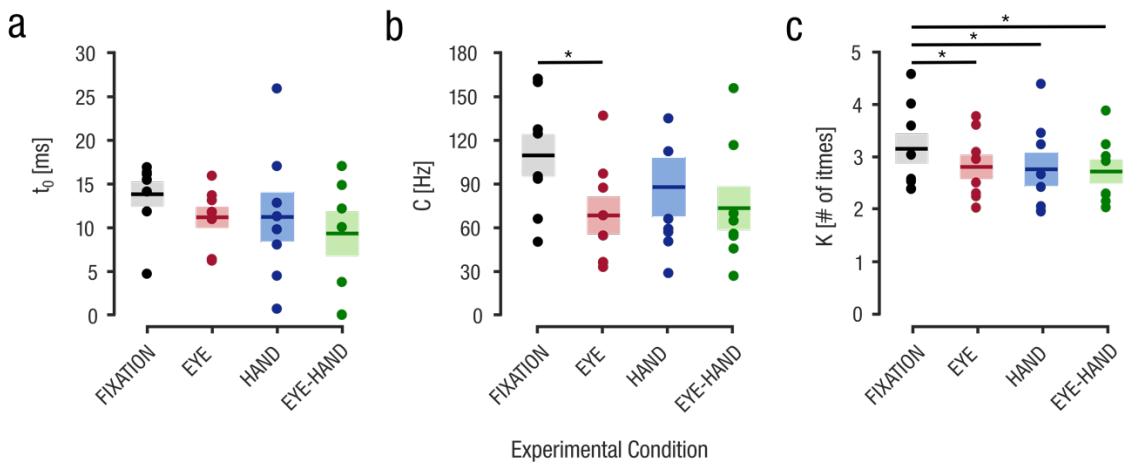

Figure 3. Extracted TVA whole report parameters t_0, C, and K of Experiment 1. TVA fitting was performed for each observer and condition separately. Dots depict (**a**) individual perceptual thresholds, (**b**) processing capacities or (**c**) vSTM storage capacities. Conventions as in Figure 2.

Experiment 2

Given our finding of constant overall attention capacity, experiment 2 was designed to assess where in the visual work space attention is withdrawn in order to allocate processing resources towards the motor targets. To this end, we introduced a reward manipulation to give participants an incentive to deploy their attention primarily to a subset of the presented items Here, we also investigate the ability to voluntarily deploy attention while performing eye-hand movement tasks. We use the term voluntary to describe the ability to deploy attention according to the reward instructions and to contrast this ability to obligatory attention shifts that occur during motor preparation.

Methods

Participants. Eight adults (age range: 25-30 years, three female) participated in this experiment (five of whom also participated in experiment 1). Participants were compensated at a fixed rate of €30 but were able to additionally earn up to €30 based on their performance in the perceptual task.

Stimuli, Apparatus, and Procedure. Stimuli, apparatus, and procedure were identical to those described for Experiment 1 with the following exceptions: (1) letters were presented either in red (50%) or blue (50%; **fig. 1b**). The different colors indicated whether a letter was associated with a high or low reward. The color-reward association was kept constant during the experiment but was counterbalanced across participants: they gained 100 points for each correctly reported high-reward letter, and ten points for each low-reward letter. Feedback on the points gained during a block was presented at the end of each block. At the end of the experiment, participants received an additional monitory reward according to the points gained during the entire experiment (18,481 points = €1). (2) The dynamic mask presented before and after letter presentation now consisted of red and blue lines. (3) Letter presentation durations were the same as in Experiment 1, but we added one longer presentation time (200 ms). (4) The *FIXATION* condition of Experiment 1 showed that the mere presentation of task-irrelevant cues did not modulate the distribution of attention (no increased performance at cued vs. uncued locations). This demonstrates that any differences between our experimental conditions are explained by motor preparation rather than visual cueing. In Experiment 2 we therefore refrained from keeping the visual input constant over the conditions and only presented movement-relevant cues (i.e. no cues in the *FIXATION* condition, only one cue in the single movement conditions, and two cues in the combined movement condition).

Experimental conditions were identical to Experiment 1 (*FIXATION*, *EYE*, *HAND*, *EYE-HAND*), and motor targets were again randomly selected out of the 6 possible stimulus locations. However, the color-reward manipulation now created different sub-conditions, given that each effector could either be directed to a high or a low reward target. Single effector conditions consisted of two sub-conditions: (1) effector on high-reward letter (*EYE+* or *HAND+*) or (2) effector on low-reward letter (*EYE-* or *HAND-*), and the combined movement condition consisted of four sub-conditions: (1) eye and hand on high-reward targets (*EYE+HAND+*), (2) eye on high-reward and hand on low-reward target (*EYE+HAND-*), (3) eye on low-reward and hand on high-reward target (*EYE-HAND+*), and (4) eye and hand on low-reward targets (*EYE-HAND-*).

Participants performed one training block (20 trials) of each condition, followed by 24 experimental blocks (minimum 70 trials each) in a randomized order (three *FIXATION*, six *EYE*, six *HAND*, and nine *EYE-HAND* blocks).

Data Analysis. We applied the same trial exclusion criteria as in Experiment 1, based on which 10.22% of the trials were excluded. Data analysis and TVA modeling procedure also were identical to Experiment 1. However, instead of comparing processing rates at different locations within the experimental conditions, here we compared them across the different experimental conditions. To assess how well participants can deploy their voluntary attention according to the reward instruction when preparing single or combined movements, we calculated their ability to select high-reward letters over low-reward letters as follows:

$$s = \frac{(v_{high} - v_{low})}{(v_{high} + v_{low})}, \quad (2)$$

where v_{high} and v_{low} denote the summed processing rates of the high and low reward items, respectively. A positive reward selectivity value indicates that more high-reward letters were correctly reported, while a negative value indicates that more low-reward items were classified. We estimated these values separately for each of the above described sub-conditions (*EYE+, EYE-,*

HAND+, HAND-, EYE+HAND+, EYE+HAND-, EYE-HAND+, EYE-HAND-), to quantify how motor preparation towards or away from high reward items affects their voluntary attentional selection.

Results

Allocation of Attention Across Experimental Conditions. In Experiment 1, when eye and hand movements were programmed simultaneously, we observed increased attention at both effector targets without any trade-off between the two. Still, the overall attention capacity did not increase with the number of active effectors. This implies that the attention benefit at the motor targets should have concomitant costs at non-target locations. To evaluate attentional trade-offs between motor targets and non-targets, we compared the respective processing rates across the different experimental conditions (**fig 4**). We replicated our findings from Experiment 1: more processing resources were allocated to motor targets as compared to non-targets. For the *EYE-HAND* condition, we again observed similarly increased processing rates at both motor targets. To assess a potential complementary withdrawal of attention from movement-irrelevant (non-target) locations, we ran a one-way rmANOVA with the factor *experimental condition* and observed a significant main effect ($F(3,21) = 24.69$; $p < 0.001$; $\eta_p^2 = 0.779$). Post-hoc pairwise comparisons revealed a significant reduction in the processing rates at non-targets between the *FIXATION* condition and the *EYE* condition ($t(7) = 5.15$; $p = 0.008$; 95% CI [5.87, 15.82]) as well as the *EYE-HAND* condition ($t(7) = 8.68$; $p < 0.001$; 95% CI [9.01, 15.76]). We also observed a significant decrease between the *HAND* and the *EYE-HAND* condition ($t(7) = 5.51$; $p = 0.005$; 95% CI [4.06, 10.18]) as well as between the *EYE* and the *HAND* condition ($t(7) = -4.25$; $p = 0.023$; 95% CI [-8.68, -2.48]).

We next assessed if there were differences in the allocation of attention between the saccade and reach targets and whether visual processing at the effector targets varied depending on whether a single or combined movement was programmed. To this end, we ran a 2 (*effector type;* eye versus hand) × 2 (*movement type;* single versus combined) rmANOVA on the estimated processing rates at the motor targets. Although there was a main effect of *movement type* (single versus combined;

$F(1,7) = 22.09$; $p < 0.002$; $\eta_p^2 = 0.759$), we did not find any significant differences based on the post-hoc pairwise comparisons (all $p > 0.133$). Neither the main effect of *effector type* (eye versus hand; $p = 0.761$), nor the interaction term ($p = 0.213$) reached significance. This suggests that the shift of attention to one effector's motor target is not hampered by movement preparation of the other effector. Instead, in order to allocate attention simultaneously to eye and hand targets, processing resources are primarily withdrawn from movement-irrelevant locations.

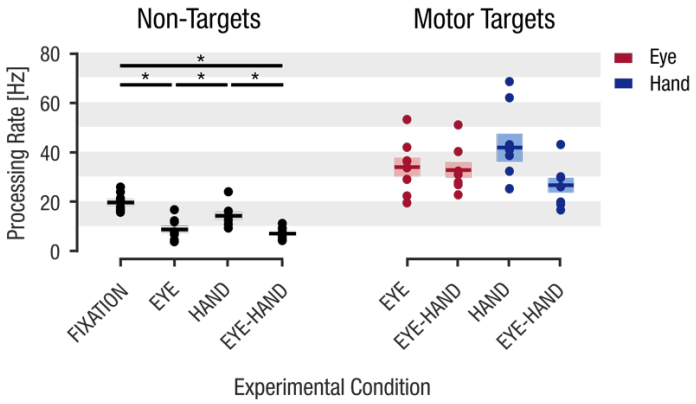

Figure 4. Processing rates (*v*-parameter) at motor targets and non-targets for each experimental condition in Experiment 2. Conventions as in Figure 2.

Reward Selectivity Across Experimental Conditions. To further investigate the selective deployment of visual attention towards the effector targets at the cost of attention withdrawal from non-targets, we quantified the ability to voluntarily deploy attention while performing goal-directed movements. To this end, we biased participants' voluntary attention by a reward manipulation: to maximize monetary reward, they should prioritize the processing of high reward letters (indicated by a specific color), and preferably name as many of these as possible. We modeled the processing rates of the high and low reward items for each sub-condition (i.e. depending on whether the movements were being prepared towards the high or low reward items). **Figure 5a** shows the fitted curves of a representative subject for the *EYE-HAND* condition. When both movements were directed to high-reward items (*EYE+HAND+*), processing rates were high for the high-reward items, compared to low-reward items. Thus, in line with the task instructions in this sub-condition this participant successfully allocated processing resources to maximize reward. However, already when only one effector was directed to a low-reward item (*EYE-HAND+* or

EYE+HAND-), this participant's ability to selectively report high over low-reward items decreased remarkably. Crucially, when both effectors targeted low-reward items (*EYE-HAND-*), the participant also preferably reported low-reward items, demonstrating that motor preparation overrode voluntarily attempts to attend elsewhere.

The extracted measurement of reward selectivity (*s*) shows that all participants exhibited a strikingly similar pattern of results (right panel of **fig. 5b**): Positive reward selectivity values indicate that more high-reward letters were correctly classified, while negative values indicate a preference for low-reward items. For all conditions, we calculated the mean and 95% confidence intervals across participants for each sub-condition to assess their difference from 0 (i.e. no selective encoding preference for neither high- nor low-reward items; **fig. 5b**). As expected, in the *FIXATION* condition participants allocated significantly more processing resources towards high-reward items than low-reward items (*mean* = 0.53; 95% CI [0.39, 0.67]), demonstrating that our reward manipulation indeed biased their voluntary allocation of attention. During the preparation of goal-directed actions, participants were able to maintain this high-reward selectivity as long as the movement(s) had to be directed to high-reward items (*EYE+*: *mean* = 0.53; 95% CI [0.41, 0.65], *HAND+*: *mean* = 0.54; 95% CI [0.40, 0.68], and *EYE+HAND+*: *mean* = 0.62; 95% CI [0.51, 0.74]). However, there was a strong reduction in the ability to prioritize high-reward over low-reward items when one movement was programmed towards a low-reward item. This was true for the single movement conditions (*EYE-*: *mean* = -0.05; 95% CI [-0.25, 0.15] and *HAND-*: *mean* = 0.12; 95% CI [-0.11, 0.34]) and the *EYE-HAND* condition (*EYE+HAND-*: *mean* = 0.21; 95% CI [0.06, 0.36] and *EYE-HAND+*: *mean* = 0.10; 95% CI [-0.01, 0.21]). Critically, when both effectors targeted low-reward items in the *EYE-HAND* condition, the allocation of attentional resources was aligned with the motor programs (i.e. more processing resources were allocated towards low-reward items; *EYE-HAND-*: *mean* = -0.38; 95% CI [-0.58, -0.18]).

This demonstrates that even when participants aim to voluntarily attend to high-reward but non-motor targets, attention nonetheless is withdrawn from the voluntarily selected items and shifts

towards the motor targets. Our limited processing resources are thus primarily allocated towards motor-targets, leaving only few resources to be voluntarily deployed to movement-irrelevant locations.

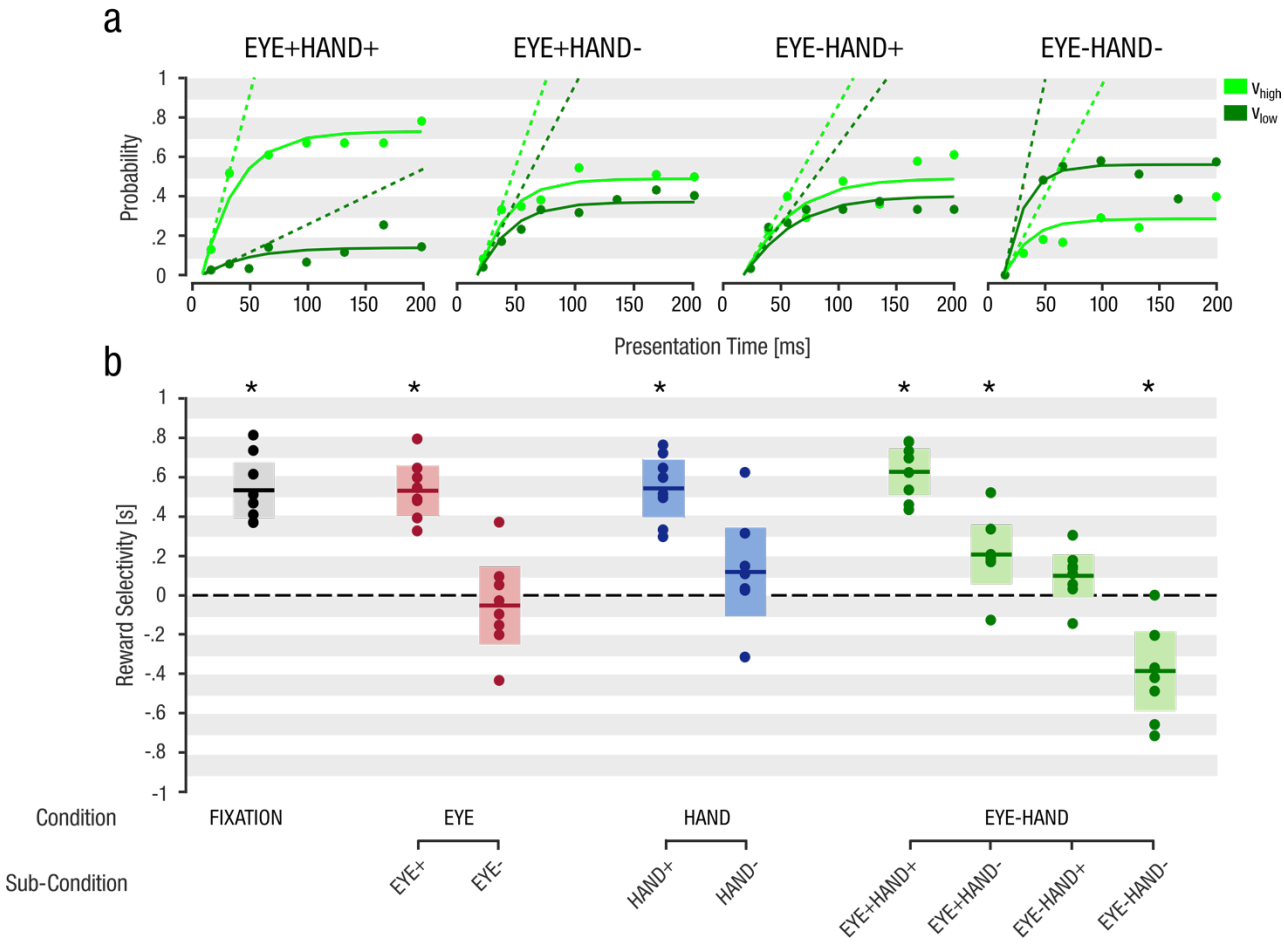

Figure 5. **(a)** Average fitting curves of a representative participant for high reward items (light green) and low reward items (dark green) in the *EYE-HAND* condition. Dashed lines represent the respective averaged processing rate. **(b)** Average reward selectivity (defined as the relative difference between high- and low- reward encoding rates) across all participants. Data was modeled for each sub-condition and participants separately. Dots represent individual subject data points. Solid lines depict the sample mean and shaded areas show 95% CI.

Discussion

We applied, for the first time, the TVA to study attentional dynamics during action preparation. In particular, we asked participants to perform eye, hand, or simultaneous eye-hand movements while we assessed visual processing at motor targets and movement-irrelevant locations in a whole report paradigm. Similar to previous studies (Hanning et al., 2018; Jonikaitis & Deubel,

2011), we found that visual attention was allocated in parallel to both effector targets during simultaneous eye-hand movement preparation. This is in contrast to previous behavioral studies observing that the eye carries more attentional weight than the hand during simultaneous eye hand movements, yielding attentional competition between the two effector systems when two separate targets have to be selected (Khan et al., 2011; Stewart, Verghese, & Ma-Wyatt, 2019). Yet, our results show that the deployment of attention towards one effector target was unaffected by the simultaneous motor preparation of the other effector system. Such parallel deployment of attention to eye and hand targets may be explained by independent, effector-specific attentional resources (Hanning et al., 2018; Jonikaitis & Deubel, 2011). A parallel attention deployment to two motor targets, however, may likewise be associated with attentional costs at movement-irrelevant locations – with the overall attention capacity being constant and not increasing with the number of active effectors.

To unravel this ambiguity, one needs to asses visual processing across the entire visual work space, including motor-targets as well as movement-irrelevant locations. Premotor visuospatial attention has been extensively investigated using sensitivity measurements (Deubel et al., 1998; Hanning et al., 2018; Hanning, Deubel, & Szinte, 2019; Jonikaitis & Deubel, 2011; Khan et al., 2011) These paradigms assessed visual attention with a single probe item presented amongst distractors and therefore measured visual attention only at one location at a time. In contrast, our premotor TVA paradigm allowed us to simultaneously assess selective processing at both, motor targets and movement-irrelevant locations, and thus to evaluate visual processing capacities over the entire space.

Our findings reveal that processing resources are primarily allocated towards motor targets, with a benefit at both targets before simultaneous eye-hand movements. Importantly, however, this is associated with attentional costs arising at non-target locations, yielding a constant attentional capacity over the entire visual work space. Likewise, a recent study also showed that attention

allocation towards the saccade goal is associated with increased suppression at uncued locations (Khan, Blohm, Pisella, & Munoz, 2015).

The neurocomputational account of the TVA (NTVA; Bundesen, Habekost, & Kyllingsbæk, 2011) describes how object selection may be implemented at the neurophysiological level. Bundesen and colleagues (2011) proposed a two-stage process of distributing attentional weights: Initially, processing resources are distributed randomly across all items in the work space. At the end of a first perceptual cycle, attentional weights are computed for each object and stored in a priority map. During a second perceptual cycle, processing resources are then selectively allocated across the objects according to the computed attentional weights. Our data fit well with this interpretation by showing a dynamic, prioritized resource allocation towards the selected motor targets. Our findings extend the object selection mechanisms proposed by the TVA during fixation. They show that motor preparation strongly influences the computation of attentional weights and reveal how processing resources are allocated across the visual work space when actively exploring and engaging with the visual environment.

Moreover, even when participants try to voluntarily attend to certain objects in the visual work space (to maximize reward), movement preparation overrides this aim: while we observed increased processing at high-reward compared to low-reward item locations when no motor action was required, this reward selectivity sharply decreased whenever an eye or hand movement was planned away from the voluntarily attended items, and completely vanished when both effectors targeted low-reward items. This demonstrates that processing resources are obligatorily shifted to motor targets, which strongly hampers the voluntary selection of visual content at non-target locations. However, while both eye and hand movement preparation interfered with participants' voluntary attention, neither of the two movements affected the benefit at the other effector target.

This apparent independence of eye and hand movement preparation seems to conflict with the commonly observed yoking between the two effector systems in free-viewing tasks (Hoffmann,

2005; Land & Hayhoe, 2001; Neggers & Bekkering, 2000). The strong spatial and temporal coupling between eye and hand movement programming has a neurophysiological basis: Overlapping networks of parietal and prefrontal cortical regions are involved in the selection of both eye and hand targets (Beurze, De Lange, Toni, & Medendorp, 2009; Levy, Schluppeck, Heeger, & Glimcher, 2007). Moreover, reach-related neuronal activity in the parietal cortex is modulated by eye position (Batista, Buneo, Snyder, & Andersen, 1999), while the activity of oculomotor neurons in supplementary and frontal eye fields is modulated by hand position signals (Mushiake, Fujii, & Tanji, 1996; Thura, Hadj-Bouziane, Meunier, & Boussaoud, 2008).

Although these studies suggest a common system for selecting eye and hand targets, our results demonstrate that during the preparation of simultaneous eye-hand movements visual attention is enhanced at both motor targets – without competition between the two. The frequently reported crosstalk between the two effector systems may thus occur at later processing states, while the initial motor target selection by means of attentional deployment is achieved by separate, effector-specific attentional mechanisms. This conjecture is supported by evidence from human imaging and neurophysiology showing that eye and hand movement preparation rely on functionally and anatomically distinct brain areas (Calton, Dickinson, & Snyder, 2002; Dickinson, Calton, & Snyder, 2003; Lawrence & Snyder, 2009; Snyder, Batista, & Andersen, 1997; Tosoni, Galati, Romani, & Corbetta, 2008; Van Der Werf, Jensen, Fries, & Medendorp, 2010). These may give rise to separate attentional enhancements via effector-specific feedback loops between frontoparietal and posterior areas (Perry & Fallah, 2017), and could thus be the basis for the simultaneous deployment of attention to both eye and hand targets during combined eye-hand movement preparation.

Extending previous findings, we show that the simultaneous enhancement of processing resources at different effector targets is associated with attentional costs at non-motor targets. Thus, a parallel allocation of visual attention to motor targets of different effectors without competition (Hanning et al., 2018; Jonikaitis & Deubel, 2011) may only be possible as long as sufficient

processing resources can be withdrawn from movement-irrelevant locations. This entails that the overall attentional capacity is constant and does not increase with the number of active effectors. Even when participants attempted to attend to movement-irrelevant locations, processing resources were obligatorily withdrawn from the voluntarily selected items and deployed towards the motor targets. Thus, premotor target selection dominates over voluntary attentional orienting when distributing limited resources across the visual work space.

TVA-based assessment of visual attention has been widely applied in both clinical (Habekost, 2001) and basic research (Bundesen & Habekost, 2014) – but solely under fixation conditions. By combining the TVA with motor tasks, our study is the first to demonstrate that this framework can also be used to assess the deployment of visual attention during motor preparation. Using the TVA to assess the ability to shift attention both covertly and overtly, during motor preparation, can help to further differentiate neuropsychological deficits and underlying pathologies. Moreover, the remarkable feature of the TVA-based assessment – the ability to quantify both overall attention capacity and attention deployment to individual objects – can be used to thoroughly analyze the allocation of attention in action contexts, overcoming limitations of previous studies that could only measure perceptual sensitivity at single stimulus location at a time.

References

Allport, D. A. (1987). Selection for action: Some behavioral and neurophysiological considerations of attention and action. In H. Heuer & H. F. Sanders (Eds.), *Perspectives on Perception and Action* (pp. 395-419). Hillsdale, NJ: Erlbaum.

Baldauf, D., Wolf, M., & Deubel, H. (2006). Deployment of visual attention before sequences of goal-directed hand movements. *Vision Research, 46*(26), 4355-4374. https://doi.org/10.1016/j.visres.2006.08.021

Batista, A. P., Buneo, C. A., Snyder, L. H., & Andersen, R. A. (1999). Reach plans in eye-centered coordinates. *Science, 285*(545), 257-260. https://doi.org/10.1126/science.285.5425.257

Beurze, S. M., De Lange, F. P., Toni, I., & Medendorp, W. P. (2009). Spatial and effector processing in the human parietofrontal network for reaches and saccades. *Journal of Neurophysiology, 101*(6), 475-484. https://doi.org/10.1152/jn.91194.2008

Bublak, P., Finke, K., Krummenacher, J., Preger, R., Kyllingsbaek, S., Müller, H. J., & Schneider, W. X. (2005). Usability of a theory of visual attention (TVA) for parameter-based measurement of attention II: evidence from two patients with frontal or parietal damage. *Journal of the International Neuropsychological Society*, *11*(7), 843–854. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/16519263

Bundesen, C. (1990). A Theory of Visual Attention. *Psychological Review, 97*(4), 523–547.

Bundesen, C., & Habekost, T. (2014). Theory of visual attention (TVA). In S. Kastner & K. Nobre (Eds.), *The Oxford Handbook of Attention* (pp. 1095–1121). New York, NY: Oxford University Press.

Bundesen, C., Habekost, T., & Kyllingsbæk, S. (2011). A neural theory of visual attention and short-term memory (NTVA). *Neuropsychologia*, *49*(6), 1446–1457. https://doi.org/10.1016/j.neuropsychologia.2010.12.006

Calton, J. L., Dickinson, A. R., & Snyder, L. H. (2002). Non-spatial, motor-specific activation in posterior parietal cortex. *Nature Neuroscience, 5*(6), 580-588. https://doi.org/10.1038/nn0602-862

Carrasco, M. (2011). Visual attention: The past 25 years. *Vision Research*, *51*(13), 1484–1525. https://doi.org/10.1016/J.VISRES.2011.04.012

Cornelissen, F. W., Peters, E. M., & Palmer, J. (2002). The Eyelink Toolbox: Eye tracking with MATLAB and the Psychophysics Toolbox. *Behavior Research Methods, Instruments, and Computers*, *34*(4), 613–617. https://doi.org/10.3758/BF03195489

Desimone, R., & Duncan, J. (1995). Neural Mechanisms of Selective Visual Attention. *Annual Review of Neuroscience*, *18*(1), 193–222. https://doi.org/10.1146/annurev.ne.18.030195.001205

Deubel, H., & Schneider, W. X. (1996). Saccade target selection and object recognition: Evidence for a common attentional mechanism. *Vision Research*, *36*(12), 1827–1837. https://doi.org/10.1016/0042-6989(95)00294-4

Deubel, H., Schneider, W. X., & Paprotta, I. (1998). Selective dorsal and ventral processing: Evidence for a common attentional mechanism in reaching and perception. *Visual Cognition, 5*(1-2), 81-107. https://doi.org/10.1080/713756776

Dickinson, A. R., Calton, J. L., & Snyder, L. H. (2003). Nonspatial saccade-specific activation in area LIP of monkey parietal cortex. *Journal of Neurophysiology, 90*(4), 2460-2464. https://doi.org/10.1152/jn.00788.2002

Duncan, J., Olson, A., Humphreys, G., Bundesen, C., Chavda, S., & Shibuya, H. (1999). Systematic analysis of deficits in visual attention. *Journal of Experimental Psychology: General*, *128*(4), 450–478. https://doi.org/10.1037/0096-3445.128.4.450

Dyrholm, M., Kyllingsbæk, S., Espeseth, T., & Bundesen, C. (2011). Generalizing

parametric models by introducing trial-by-trial parameter variability: The case of TVA. *Journal of Mathematical Psychology*, *55*(6), 416–429. https://doi.org/10.1016/j.jmp.2011.08.005

Engbert, R., & Mergenthaler, K. (2006). Microsaccades are triggered by low retinal image slip. *Proceedings of the National Academy of Sciences of the United States of America, 103*(18), 7192-7197. https://doi.org/10.1073/pnas.0509557103

Finke, K., Bublack, P., Krummenacher, J., Kyllingsæk, S., Müller, H. J., & Schneider, W. X. (2005). Usability of a theory of visual attention (TVA) for parameter-based measurement of attention I: Evidence from normal subjects. *Journal of the International Neuropsychological Society, 11*(7), 832-842. https://doi.org/10.1017/S1355617705050976

Habekost, T. (2015). Item Based Fitting of Partial Report Data. *Frontiers in Psychology, 6,* Article 290.

Hanning, N. M., Aagten-Murphy, D., & Deubel, H. (2018). Independent selection of eye and hand targets suggests effector-specific attentional mechanisms. *Scientific Reports*, *8*(1), 1–8. https://doi.org/10.1038/s41598-018-27723-4

Hanning, N.M., Deubel, H., & Szinte, M. (2019). Sensitivity measures of visuospatial attention. *Journal of Vision, 19*(12), Article 17.

Horstmann, A. & Hoffmann, K.P. (2005). Target selection in eye – hand coordination : Do we reach to where we look or do we look to where we reach ? *Experimental Brain Research, 167*(2), 187–195. https://doi.org/10.1007/s00221-005-0038-6

Jonikaitis, D., & Deubel, H. (2011). Independent allocation of attention to eye and hand targets in coordinated eye-hand movements. *Psychological Science*, *22*(3), 339–347. https://doi.org/10.1177/0956797610397666

Khan, A. Z., Blohm, G., Pisella, L., & Munoz, D. P. (2015). Saccade execution suppresses discrimination at distractor locations rather than enhancing the saccade goal location. *European Journal of Neuroscience*, *41*(12), 1624–1634. https://doi.org/10.1111/ejn.12923

Khan, A. Z., Song, J. H., & McPeek, R. M. (2011). The eye dominates in guiding attention during simultaneous eye and hand movements. *Journal of Vision, 11*(1), Article 9. https://doi.org/10.1167/11.1.1

Kleiner, M., Brainard, D., Pelli, D., Ingling, A., Murray, R., & Broussard, C. (2007). What's new in Psychtoolbox-3. *Perception, 36*(14), 1-16.

Kowler, E., Anderson, E., Dosher, B., & Blaser, E. (1995). The role of attention in the programming of saccades. *Vision Research, 35*(13), 1897-1916. https://doi.org/10.1016/0042-6989(94)00279-U

Land, M. F., & Hayhoe, M. (2001). In what ways do eye movements contribute to everyday activities? *Vision Research, 41*(25-26), 3559-3565. https://doi.org/10.1016/S0042-6989(01)00102-X

Lawrence, B. M., & Snyder, L. H. (2009). The Responses of Visual Neurons in the Frontal Eye Field Are Biased for Saccades. *The Journal of Neuroscience*, *29*(44), 13815-13822. https://doi.org/10.1523/JNEUROSCI.2352-09.2009

Levy, I., Schluppeck, D., Heeger, D. J., & Glimcher, P. W. (2007). Specificity of human cortical areas for reaches and saccades. *The Journal of Neuroscience, 27*(17), 4687-4696. https://doi.org/10.1523/JNEUROSCI.0459-07.2007

McAvinue, L. P., Habekost, T., Johnson, K. A., Kyllingsbæk, S., Vangkilde, S., Bundesen, C., & Robertson, I. H. (2012). Sustained attention, attentional selectivity, and attentional capacity across the lifespan. *Attention, Perception, and Psychophysics*, *74*(8), 1570–1582. https://doi.org/10.3758/s13414-012-0352-6

Montagnini, A., & Castet, E. (2007). Spatiotemporal dynamics of visual attention during

saccade preparation : Independence and coupling between attention and movement planning. *Journal of Vision, 7*(14), Article 8. https://doi.org/10.1167/7.14.8.Introduction

Mushiake, H., Fujii, N., & Tanji, J. (1996). Visually guided saccade versus eye-hand reach: Contrasting neuronal activity in the cortical supplementary and frontal eye fields. *Journal of Neurophysiology, 75*(5), 2187-2191. https://doi.org/10.1152/jn.1996.75.5.2187

Neggers, S. F. W., & Bekkering, H. (2000). Ocular gaze is anchored to the target of an ongoing pointing movement. *Journal of Neurophysiology, 83*(2), 639-651.

Nissens, T., & Fiehler, K. (2018). Saccades and reaches curve away from the other effector's target in simultaneous eye and hand movements. *Journal of Neurophysiology*, *119*(1), 118–123. https://doi.org/10.1152/jn.00618.2017

Perry, C. J., & Fallah, M. (2017). Effector-based attention systems. *Annals of the New York Academy of Sciences*, *1396*(1), 56–69. https://doi.org/10.1111/nyas.13354

Rolfs, M., Lawrence, B. M., & Carrasco, M. (2013). Reach preparation enhances visual performance and appearance. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*(1628). https://doi.org/10.1098/rstb.2013.0057

Snyder, L. H., Batista, A. P., & Andersen, R. A. (1997). Coding of intention in the posterior parietal cortex. *Nature, 386*(6621), 167-170. https://doi.org/10.1038/386167a0

Stewart, E. E. M., Verghese, P., & Ma-Wyatt, A. (2019). The spatial and temporal properties of attentional selectivity for saccades and reaches. *Journal of Vision*, *19*(9), Article 12. https://doi.org/10.1167/19.9.12

Thura, D., Hadj-Bouziane, F., Meunier, M., & Boussaoud, D. (2008). Hand position modulates saccadic activity in the frontal eye field. *Behavioural Brain Research, 186*(1), 148-153. https://doi.org/10.1016/j.bbr.2007.07.035

Tosoni, A., Galati, G., Romani, G. L., & Corbetta, M. (2008). Sensory-motor mechanisms in human parietal cortex underlie arbitrary visual decisions. *Nature Neuroscience, 11*(12), 1446-1453. https://doi.org/10.1038/nn.2221

Van Der Werf, J., Jensen, O., Fries, P., & Medendorp, W. P. (2010). Neuronal synchronization in human posterior parietal cortex during reach planning. *The Journal of Neuroscience, 30*(4), 1402-1412. https://doi.org/10.1523/JNEUROSCI.3448-09.2010