A Dedicated Binding Mechanism for the Visual Control of Movement

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Summary

The human motor system is remarkably proficient in the online control of visually guided movements, adjusting to changes in the visual scene within 100 ms [1–3]. This is achieved through a set of highly automatic processes [4] translating visual information into representations suitable for motor control [5, 6]. For this to be accomplished, visual information pertaining to target and hand need to be identified and linked to the appropriate internal representations during the movement. Meanwhile, other visual information must be filtered out, which is especially demanding in visually cluttered natural environments. If selection of relevant sensory information for online control was achieved by visual attention, its limited capacity [7] would substantially constrain the efficiency of visuomotor feedback control. Here we demonstrate that both exogenously and endogenously cued attention facilitate the processing of visual target information [8], but not of visual hand information. Moreover, distracting visual information is more efficiently filtered out during the extraction of hand compared to target information. Our results therefore suggest the existence of a dedicated visuomotor binding mechanism that links the hand representation in visual and motor systems.

Results and Discussion

Skilled motor control demands the simultaneous processing of different sources of visual information. For example, when several basketball players jump for the ball at the same time, a player must track visual information pertaining to the target (e.g., hands of the basketball and the controlled limb) while ignoring distractive visual information (e.g., other players’ hands or the background). How does the visuomotor system accomplish this task efficiently? In perceptual tasks, selection of relevant sensory information is considered to be a function of attention [7]. Likewise, one might suggest that visual attention also facilitates processing of all relevant visual information during the control of movement. Directing visual attention to the target of a reach accelerates the initiation of the movement, and overt attention (gaze direction) is therefore typically focused on this target [9, 10]. Consequently, covert visual attention would have to be allocated to the moving limbs to achieve accurate feedback control. When one reaches with both hands to two separate targets simultaneously [11], for instance, this division of resources would place high demands on a limited-capacity visual attention system [7].

To study the role of attention in visual feedback control, we challenged the visuomotor system with a bimanual reaching task. Participants held a robotic manipulandum with each hand and moved these simultaneously to two targets presented in the left and right visual fields while keeping their eyes fixated at a central location (enforced via eye tracking). During the task, participants’ hands were occluded by a horizontally mounted monitor, which displayed the cursors and targets (Figure 1A). The task therefore required participants to simultaneously process visual information from two targets and two cursors. To test whether spatial visual attention influences the processing of visual target and hand information during online control, we manipulated the locus of attention via exogenous cuing. Immediately after the onset of the movement, covert attention was attracted by briefly increasing the luminance [12] of a target or cursor (“flashes”; see Figure 1A). We assessed the influence of attention by displacing the position of one of the targets or cursors perpendicular to the reaching direction 100 ms after the flash [13] (Figure 1A). The side of the displacement was independent of the side of the preceding attention manipulation, but it occurred always on the same object type (target or cursor) as the attentional cue. The displacement evoked an automatic feedback response with the corresponding hand: rightward for target displacements to the right and leftward for cursor displacements to the right [1, 4, 15]. The forces with which participants pushed into “force channels” [16] during interspersed probe trials provided a sensitive assay of the early corrective motor response [1].

We found fast (onsets around 165 ms) and consistent responses to both target and cursor displacements. These indicate that the sensorimotor system, rather than relying exclusively on proprioceptive or efference copy information, is exquisitely sensitive to visual feedback from the hands [17, 18], even when it tracks both hands simultaneously. The force response to target displacements (Figures 1B and 1D) was modulated by the locus of attention. Displacements preceded by the exogenous cue elicited significantly stronger initial responses (for statistical details, see Figure 1D) and produced earlier onsets of the correction (Figure 1E) than uncued displacements. The size of the attentional modulation on feedback responses was of similar magnitude as for simple reaction time tasks [19]. In contrast, exogenous cuing did not modulate the responses to cursor displacements (Figures 1C–1E). The interaction for displacement type (target or cursor) × attention was significant for both response strength ($F_{1,13} = 7.129, p = 0.019$) and onset ($F_{1,13} = 10.005, p = 0.008$).

To corroborate these findings, we conducted a second experiment in which we manipulated covert attention endogenously using a secondary perceptual task. At the start of a trial, we presented an arrow near fixation that pointed to the left or right (cue validity for the perceptual task: 83%). During the reaching movement, the luminance of one of the targets (or, in separate blocks, the luminance of one of the cursors) was subtly changed for 350 ms. After completing the movement, participants reported whether the luminance had...
increased or decreased. During the movement, we probed feedback control by displacing either the left or right target (or, in separate blocks, the cursor) 100 ms before the luminance change. Accuracy on the brightness discrimination task was better on the cued side ($F_{1,18} = 18.449, p < 0.001$; Figure 2A), demonstrating successful attention manipulation both for the cursor and target conditions. Corrective motor responses to target displacements were also significantly greater for the attended side (Figure 2B includes statistical details). In contrast, the response to cursor displacements was not modulated by the cue. As in the exogenous case, the displacement type (target or cursor) $\times$ attention interaction was significant ($F_{1,18} = 5.030, p = 0.038$). The time of response onsets revealed a similar pattern, although here the interaction did not reach significance (Figure 2C).

These results indicate that both exogenous and endogenous visual attention modulate the processing of target information [9]. In contrast, the processing of visual information about the moving limb, although fast and efficient, seemed to be independent of either attentional manipulation. Our failure to detect an effect of the attentional modulation on responses to cursor perturbations is unlikely to be caused by a simple lack of statistical power. The power for detecting an effect of the size of the attentional modulation on responses to target displacements was >80% with our design (82.1% and 98.7% for experiments 1 and 2, respectively). Furthermore, the significant interaction shows that an attentional modulation effect was clearly larger for target displacements than for cursor displacement—if the latter was present at all. Finally, the absence of attentional modulation on cursor displacement responses is unlikely to be a result of a ceiling effect limiting the size of the maximal response to cursor displacements. In an additional control experiment (Supplemental Information available online), we introduced visual distractors alongside targets and cursors to reduce the size of the feedback response. Even though the demand on visual processing increased, additional allocation of visual attention facilitated only target, but not cursor, processing, ruling out a ceiling effect. We therefore suggest that the binding of reafferent visual information about the movement to the corresponding motor command is achieved without (or at least compared to target processing with much less) aid of visual attention. Therefore, we propose the existence of a separate visuomotor binding mechanism that confers a privileged status on visual information representing the kinematics of a moving limb.

If different mechanisms underlie attentional and visuomotor binding, they may also differ in their ability to filter out and ignore distracting objects. Due to the limited capacity of visual attention [7], filtering constitutes a problem in complex natural
A dedicated visuomotor binding mechanism during voluntary movements would explain the efficiency and speed with which humans can execute multiple goal-directed movements at the same time [11]. This is not because visuomotor binding provides faster responses than other processes, but because its independence of visual attention frees those limited resources for allocating them to the current target during reaching [9] and to potential alternative targets or interfering objects [8]. Why the brain has developed a specialized mechanism for processing reafferent visual information, instead of relying on the general-purpose mechanisms of attention, remains to be answered by future research. We can only speculate that the necessity to react very rapidly to divergent visual information about both the target and the hand has been evolutionary important enough to justify the development of a specialized mechanism. While attention is already involved in the detection and selection of targets before movement onset [8, 9], it seems sensible that it should retain this function during online control, supporting the flexibility of the visuomotor system to adjust movement goals midreach. In contrast, the effector is rarely changed within a movement, and visuomotor binding heavily depends on efference copy and proprioceptive information. These special characteristics may have further promoted the emergence of a dedicated process.

Note that we are not claiming that processing of the target during the online control of movement is conscious or voluntary. On the contrary, there is substantial evidence that online
corrections to target displacements can bypass voluntary control \[4, 21\] and even occur without conscious awareness \[15\]. The same has been shown for processing of visual hand information \[1, 20\]. What we show here is that this automatic target processing can be facilitated by the allocation of visual attention—whereas the processing of hand information cannot. Thus, our results demonstrate that even though processing of visual target and hand information share some features regarding their automatic and involuntary nature, the processing of visual hand information appears to occur through a dedicated channel that is uninfluenced by the allocation of visual attention.

We suggest that the visuomotor binding mechanism detects spatiotemporal correlation between objects in the visual scene and internal state estimates of moving limbs. This internal estimate is informed by proprioceptive information, and the predictions arising from a forward model through an efference copy \[22\] of the executed motor commands \[23–25\]. Visuomotor binding is complicated by the fact that the spatial relationship between movement and visual consequences is often highly task dependent. However, the ease with which we handle tools \[28\] or remotely controlled objects such as computer cursors \[27\] suggests that it is a highly flexible process that can learn new mappings between motor commands and visual outcomes. The factors influencing these adaptive processes and their relationship to the adaptation of dynamic forward models \[28\], however, have yet to be elucidated.

Assignment of visual input to one’s own action has been debated extensively as “intention or action attribution” or “agency” in the context of conscious perception \[29, 30\]. These studies show that sensory events judged to be consequences of one’s own actions are perceived differently from sensory events judged to arise from external causes \[31–33\]. Our results emphasize that the detection of visual stimuli pertaining to our own movements is a fundamental process for the online control of reaching movements. The link between actions and visual consequences allows the motor system to respond rapidly to visual feedback signaling reach errors, even in the face of potentially distracting visual information as present in naturalistic visual scenes. Visuomotor binding...
is most likely a phylogenetically old mechanism common to all species that rely on vision for movement guidance. It must therefore constitute a central concept in theories of visuomotor feedback control. Indeed, it is possible that this process forms the basis upon which the percept of a “sense of agency” is founded.

The proposal of a dedicated mechanism raises the question of how visuomotor binding is implemented in the nervous system. Visual attention arises through top-down influences of parietal and prefrontal areas onto sensory regions, increasing signal-to-noise in these regions through an increase in sensitivity and contrast gain of relevant neurons [34–37]. Visuomotor binding could act through a conceptually similar yet independently implemented mechanism. For example, one may hypothesize that the link is established by neural synchronization between sensory areas and corresponding motor cortical regions [38] or upstream premotor and parietal regions coding visual space near the hand [39]. Sudden sensory changes would then be directly transmitted to the respective motor circuits for rapid feedback control.

While more work remains to be done to further characterize the proposed mechanisms behaviorally and shed light on its neural implementation, our current results provide the first strong evidence for the existence of a visuomotor binding mechanism that is dissociable from general visual attention. This specialized mechanism constitutes the connecting link between sensory and motor systems by providing a privileged channel for reafferent visual information.

Experimental Procedures

Further details about the experimental procedures and the control experiment are described in the Supplemental Information.

Supplemental Information

Supplemental Information includes Supplemental Experimental Procedures and one figure and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2014.02.030.

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Supplemental Experimental Procedures

Participants

Neurologically healthy right-handed [S1] volunteers were recruited from an internal experiment database. All participants provided prior written informed consent and were paid for participating. They were naïve to the purpose of the experiment and debriefed afterwards. The UCL research ethics committee approved all experimental procedures.

Apparatus and visual scene

Participants were seated comfortably in front of a virtual environment setup, leaning slightly forward with their forehead supported by a chin and forehead rest. They made 20cm reaching movements away from and towards their body while holding onto a robotic manipulandum (update rate 1kHz; position and force data sampled at 200Hz) with each hand (experiments 1 and 2) or with only their right hand (experiment 3). Movements involved shoulder, elbow, and wrist in the horizontal plane at chest height. An LCD monitor (update rate 60Hz) mounted horizontally above the manipulanda prevented direct vision of the hands, but allowed participants to view the visual scene on the monitor. An eye tracker (EyeLink 1000, SR Research Ltd., Kanata, Ontario, Canada) recorded the left eye’s position with 200Hz and the data was processed in real-time by the control PC to provide feedback about eye fixation (see below).

The visual display included cursor(s) indicating the hand position(s) (filled circle(s) of 0.6cm diameter), located vertically above the real positions of the hand(s). Reaching movements for each hand were executed from a start box to a target box (filled square(s), 0.6cm size, 6cm distance to the right (and left) from body midline), alternating between up- and downward movements. Fixation had to be maintained on a white fixation cross (0.5cm) located at body midline at a height such that all visual perturbations occurred at the same eccentricity from central fixation.
We applied two types of perturbation during the reaching movements. Target displacements consisted of a 2cm displacement of the visual target in the lateral direction (left or right in the x-direction), ramped over a 50ms interval. Cursor displacements consisted of a 2cm displacement of the visual cursor in the lateral direction. The necessary correction to both perturbation types was equal in size, but opposite in direction, i.e. a target displacement to the right caused a corrective response to the right while a cursor displacement to the right caused a corrective response to the left. Both perturbations could be easily detected and participants were informed about their occurrence before the experiment started. However, responses to such perturbations are highly automatic and immune to voluntary processes [1, 4, S2].

**Eye fixation control**

The position(s) of the fixation cross(es) in eye coordinates were obtained from each participant with a calibration procedure before the start of the experiment. To avoid frequent re-calibration or problems due to drift or head movements, we used a combined manual / automatic procedure to ensure eye fixation throughout a trial. During the training, the experimenter checked the mean eye position of trials reported as valid (obtained from the automatic procedure, see below) for discrepancies between expected and actual mean eye position. Participants fixating elsewhere were reminded to keep their eyes on the fixation cross. During the experiments, we relied on the automatic procedure, but sample inspection ensured that the participants did not change their strategy and fixated somewhere else. The automatic procedure required that 80% of the recorded eye tracking data within the movement phase of a trial was technically valid (i.e. at most 20% missing values received from the eye tracker). From the validly recorded data, 68.2% was required to be within 1mm (in screen coordinates) of the mean eye position of the trial. Trials not fulfilling these criteria were automatically rejected as invalid eye fixation trials, and repeated. Because eye fixation needs a visual anchor to be stable [S3], we can exclude the possibility that the eyes rested on the blank screen adjacent to the fixation cross or moved around if a trial was accepted by the automatic procedure.
General procedure

Participants initiated a trial by moving the cursor(s) into the start while maintaining eye fixation. After 350ms, the target(s) appeared at 20cm distance from the start positions. Participants were instructed to initiate fast and accurate reaching movements toward the target(s) when the fixation cross changed shape (two small circles were added centrally over the fixation cross), which happened 2.3s after the target(s) appeared. The trial ended when hand velocity dropped below 3.5cm/s for at least 40ms. A trial was considered valid when eye fixation was maintained, movement duration was shorter than 800ms, and maximum velocity ranged between 50 and 80cm/s. Valid trials with endpoint accuracy of at least 7mm were rewarded with one point per hit target, an animated “explosion”, and a pleasant tone. A running score was displayed at the top of the screen. Feedback about trial performance (accuracy / velocity / eye fixation) was given via a color scheme at the end of each trial. Participants were encouraged to use this visual feedback to adjust their performance.

Invalid trials constituted 15%/10%/20% of all executed trials (experiment 1/2/3) and were repeated by randomly intermixing them into the remaining trials of the current experimental block.

In half of the trials, a “force channel” restricted movements, guiding the hands on a straight path to the targets. The force channel was implemented with a spring-like force of 7000N/m applied in the lateral direction. The force with which participants pressed into the channel provided a more sensitive assay of the feedback triggered responses than position data from unconstrained trials [1, 15]. The sensitivity is similar to velocity data but as force is measured directly, and not differentiated, no additional noise is introduced. On channel trials, the target or cursor was displaced back after 350ms to enable participants to reach the target. On non-channel trials, the target and cursor displacements remained, requiring participants to correct for the perturbations. We refrained from using force channel trials during training blocks in order to avoid a possible attenuation of the feedback response [1].
Experiment 1: Exogenous cueing of attention

Fourteen participants (8 female, 23.4±3.8 years) completed one experimental session (~1.5 hours). After one training block, they performed 8 experimental blocks of 80 trials. Each block consisted of the randomized permutation of all experimental conditions: perturbation type (target/cursor) x movement (up-/downwards alternating) x channel (y/n) x flash side (left/right hemi-field) x 5 displacement conditions. Four different displacements (left/right hemi-field x leftward/rightward) and one condition without displacement were tested. The cursors, start and target boxes were dark grey throughout the trials. When the mean tangential velocity of both hands exceeded 3.5cm/s (“mvmt onset” in Fig. 1a), the corresponding object (cursor or target) alternated its color between white and gray twice within 50ms (“flash” in Fig. 1a). This exogenous cue was presented on the left or right cursor on blocks with cursor displacements, and on the left or right target on blocks with target displacements. The displacement occurred 100ms after triggering the flashes, which corresponded to roughly 5cm into the movement.

Experiment 2: Endogenous cueing of attention

Nineteen participants (13 female, 24.0±4.7 years) completed a pre-test and two experimental sessions (~2 hours each). During the pre-test, either one cursor or one target changed its brightness for 350ms during the reaching movement. Participants’ task was to decide after the movement whether luminance had increased or decreased during the reach (2 alternative forced choice task). By using different levels of brightness change, we determined a contrast level that yielded a perceptual performance of $d' = 0.3$ (separately for cursors and targets) for each individual participant, which was then used throughout the experiment. One additional participant was pre-tested but excluded from the experiment because of chance performance up to the highest contrast level.

The experiment consisted of 16 blocks of 48 trials. The site of color change and displacement (cursor vs. target condition) alternated between blocks. Thus, participants could concentrate on either the
cursors or targets for the perceptual task. Each block contained 50% non-channel trials used for assessing perceptual performance. These consisted of a randomized permutation of all experimental perception conditions: movement (up-/downwards, alternating) x cuing (left/right) x brightness change (1/3 incongruent, 2/3 congruent with cue) x change direction (brighter/darker). The remaining 50% were channel trials, used for assessing fast feedback responses to displacements, with the randomized permutation of all experimental reaching conditions: movement (up-/downwards, alternating) x cuing (left/right; brightness change was always congruent with the cue) x side of displacement (left/right) x direction of displacement (left/right/none). The cursors, start and target boxes were medium grey throughout the trials. An arrow pointing left- or rightwards adjacent to the fixation cross served as central cue. In perturbation trials, the displacement occurred when both hands had moved an average 5cm in the forward direction. The brightness change occurred 100ms after the displacement (or the point in time when a displacement would have occurred for unperturbed trials) such that it could not interfere with the early response to the displacement. After each successful reach, participants made the perceptual judgment.

**Experiment 3: Distractor interference in a complex visual scene**

Ten participants (5 female, 22.0±2.8 years) completed two experimental sessions (~1.5 hours each). After four training blocks (up-/downwards without distractors, up-/downwards with distractors), they carried out 20 experimental blocks of 76 trials. Two additional participants were trained but excluded from the second day of the experiment because they performed poorly (best block fewer points than the average block score). The target movement ended in the middle of the screen at about the height of the fixation cross. Participants had the goal to terminate their cursor movement as close to the target endpoint as possible (Fig. 3a). In order to maintain the length of the reaching movement at 20cm while still using the same visual field as in the first two experiments, we compressed the visual scene by factor 2 in the y-direction. Therefore, both cursor and target moved about 10cm visually while the hand moved 20cm physically. At the height of the start box, the cursor was located vertically above the hand. Thus, we alternated between up- and downward blocks to
keep the visuo-motor mapping constant within a block. The order of up- and downward blocks was
counterbalanced across participants. Even though adaptation to a constant visuo-motor gain
mapping happens virtually instantly and generalizes across directions [S4], we started each block
with four unperturbed and undistracted movements to allow for adaptation. The remaining 72 trials
of each block consisted of the randomized permutation of all experimental conditions: perturbation
type (target/cursor) x channel (y/n) x displacements (18 conditions). Without distractors, there were
3 displacement conditions (to the left/right/none). With distractors (1, 2, or 4), there were 5
displacement conditions (cursor/target to the left or right, distractor to the left or right, or none).

The cursors, start and target boxes were white throughout the trials. In distractor trials, the
distractors appeared together with the target. The distractor starting positions were uniformly
distributed around the target/cursor initial positions, ±4cm horizontally and ±2cm vertically, with a
minimum horizontal distance of 1.2cm. The target and the distractors moved with a minimum jerk
profile in y-direction [S5] while the x-position remained constant. The onset time and movement
time for each target and distractor were sampled independently from the measured distribution of
the RT and MTs of each individual participant (Fig. 3b). Thus, the motion of the target and distractors
mimicked the cursor motion, but their velocity profiles in y-direction correlated only partially with
that of the target or cursor (r=0.73±0.01). The actual cursor and target had a red border from target
appearance until the cue to initiate the movement. In perturbation trials, the displacement occurred
when the corresponding hand had moved 2cm in the forward direction.
**Statistical analysis**

As invalid trials were repeated within each block, we averaged over 8/8/10 repetitions (experiment 1/2/3) for each condition and participant. All position and force traces were aligned temporally to the onset of the visual perturbations, or, for unperturbed trials, the point in time when the perturbation would have occurred. The measured lag of 50ms between commanded visual change and the real visual change on the screen due to processing time in the graphical output and the screen refresh rate was taken into account for the analysis.

To assess corrective reaching responses, we measured the lateral forces exerted into the channels (perpendicular to the reaching direction, cf. Fig. 1b,c, 3c,d). Response onsets (Fig. 1b,c,e, 2c, 3c,d) for each subject and condition were determined by performing t-tests between the force traces of all leftward and rightward corrections until at least 4 consecutive tests revealed significant differences ($p < .05$). The time stamp of the first of those 4 consecutive tests was taken as response onset [S6, S7]. For all further analyses, we mirrored the force traces for which we expected a negative force response and then averaged over perturbation directions. This automatically removed any constant force profiles caused by the biomechanical properties of the arm and robot. Furthermore, we pooled the data for the conditions of no interest, namely up- and downward movements, and the right and left hand for the first two experiments. To obtain a time-averaged single measure for the early response strength, we averaged the forces around mean onset time across no distractor conditions and participants (from 30ms before until 70ms after response onset, Fig. 1b,c, 3c,d).

For statistical assessment, we used repeated-measures ANOVA (within each experiment), and two-tailed t-tests between conditions (paired where applicable). Corrections for multiple comparisons were performed using Bonferroni corrections where necessary.
Supplemental Control Experiment

To exclude the possibility that the lack of attention effect on the processing of hand information resulted from a ceiling effect, we conducted a control experiment replicating Experiment 1. Within this experiment, we tested an additional control condition, in which we suppressed the overall responsiveness to the visual displacements by introducing a distractor for each target and each cursor. The movement of the cursor distractors was implemented in the same manner to those in Experiment 3, and the target distractor were stationary at the same spatial distance as the cursor distractors. The overall response strength was indeed decreased by introducing distractors (Fig. S1).

In fact, the responses to target and cursor displacements were suppressed to similar amounts as expected for very complex scenes comparable to the 4-distractor condition in Experiment 3. The response pattern regarding the attention manipulation, however, replicated our previous results from Experiments 1 and 2: Only the force response to target displacements was modulated by the locus of attention. Displacements preceded by the exogenous cue elicited significantly stronger initial responses (for statistical details see Fig. S1) than displacements that were uncued. In contrast, exogenous cuing did not modulate the responses to cursor displacements for any distractor condition. This is corroborated by the significant interaction ($F_{1,8}=8.554; p=.019$) for displacement type (target/cursor) x attention, whereas the three-ways interaction also including distractors (without/with) was not significant ($F_{1,8}=0.261; p=.624$). These results clearly show that processing of visual hand information is not modulated by visual attention, even when there is the possibility that it increases the response strength in the presence of distractors, as shown in the target condition.

![Figure S1](image-url)  
**Figure S1** Responses to target and cursor perturbations in the control experiment. Related to “Results and Discussion”. Attention had a significant effect on the response strength to target perturbations (without distractors: $t_8=4.744; p<.001$; with distractors: $t_8=2.448; p=.020$), but no effect on the response strength to cursor perturbations (both $p>.1$). Error bars denote 1 SEM between participants. * $p<.05$, ** $p<.01$. 

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Supplemental References


