Concurrent visual and motor selection during visual working memory guided action

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Visual working memory enables us to hold onto past sensations in anticipation that these may become relevant for guiding future actions. Yet laboratory tasks have treated visual working memories in isolation from their prospective actions and have focused on the mechanisms of memory retention rather than utilization. To understand how visual memories become used for action, we linked individual memory items to particular actions and independently tracked the neural dynamics of visual and motor selection when memories became used for action. This revealed concurrent visual-motor selection, engaging appropriate visual and motor brain areas at the same time. Thus we show that items in visual working memory can invoke multiple, item-specific, action plans that can be accessed together with the visual representations that guide them, affording fast and precise memory-guided behavior.

Effective behavior requires detailed sensory information to guide action, but this information is often unavailable to our senses at the time actions become relevant, for example, because visual objects have become occluded or because we have looked away. Visual working memory is the core cognitive function that bridges potentially relevant visual sensations to anticipated future actions. Despite this strong conceptual link between visual working memory and motor control, popular laboratory tasks of visual working memory (for example, refs. 1–6) tend to consider visual representations in isolation from their prospective actions, while tasks of action preparation (or ‘motor’ working memory; for example, refs. 7–9) tend to neglect the potential contribution of visual memory representations that may guide action. In addition, while the cognitive and neural mechanisms of working-memory retention have received ample investigation, little remains known about the mechanism of working-memory utilization—that is, when working memories are actually ‘put to work’10,11. To understand how visual working memories guide action requires investigating how both visual memories and their corresponding actions become selected to support memory-guided behavior. To this end, we developed a novel laboratory task of working memory in which we linked individual memories to particular actions. Through a carefully balanced task-design, we were able to leverage electroencephalography (EEG) to individuate and independently track human brain activity related to the visual location and the response hand that were uniquely associated with the probed memory item that became relevant for action.

Results

Twenty-five healthy human volunteers performed a working-memory task (Fig. 1a) that fused conventional visual and motor working-memory tasks. One of two colored visual items (tilted bars) was equally probable to become used for action after a brief memory delay (randomly drawn between 2 and 2.5 s). A color change of the central fixation cross (the memory probe) prompted participants to select the color-matching item to reproduce its tilt as accurately as possible.

To link visual memory items to specific actions in a controlled laboratory setting, the hand required for responding was directly linked to the tilt of the probed item. Participants pressed a key with their right (left) index finger to initiate a clockwise (counterclockwise) rotation of a visualized response dial and released the key when the dial reached the desired tilt, terminating the response. The central response dial always started in the vertical position and could be rotated by maximally ±90°. As a consequence, a leftward (rightward) tilted item could only ever be accurately reported with a left (right) key press. Each trial contained one leftward and one rightward tilted item (each randomly tilted between 20 and 70°) that were randomly allocated to the left and right position on the screen. Item selection (after the memory probe) could thus take place between two visual locations and between two potential response hands.

Participants relied on detailed information of the probed memory item to guide their actions. Figure 1b shows response densities, which varied systematically as function of tilt direction (that is, response hand) and magnitude (that is, response duration). Reproduction errors (Fig. 1c) were on average 14.14 ± 0.84° (M ± s.e.m.) and it took participants on average 755.76 ± 52.29 ms to select the relevant item and to initiate the appropriate action (Fig. 1d).

We asked how and when visual representations and their corresponding actions became selected after the memory probe to support memory-guided behavior. We considered three alternative scenarios (Fig. 1e–g). (1) The brain may initially focus on only the visual information and wait for the relevant visual representation to be selected before planning the appropriate action, yielding a serial pattern of visual-then-motor selection (Fig. 1e). Such a model is implicit in conventional studies of visual working memory in which memory items are deliberately isolated from particular actions during retention1–4. (2) Alternatively, visual representations may be transformed into motor plans soon after encoding and become obsolete, such that the memory probe directly triggers motor selection (Fig. 1f). Such a model is implicit in conventional studies of motor working memory, in which actions are instructed by simple sensory cues regarding, for example, the location of a prospective reach or saccade target2–9. (3) Finally, we hypothesized that, when potential actions rely on detailed sensory representations (such as precise visual orientation in our task), visual and motor representations may be held available...
Articles jointly and thereby afford simultaneous (that is, parallel, as opposed to serial) sensory and motor selection when an item becomes relevant for action (Fig. 1g).

To arbitrate among these scenarios, we capitalized on the high temporal resolution of electrophysiological brain recordings to track the unfolding of visual and motor selection during the post-probe time period of working memory utilization (sometimes referred to as ‘output gating’11). We focused on item location and required response hand as the visual and motor attributes, because these are particularly tractable in non-invasive human electrophysiology. Because item location and required response hand were orthogonally manipulated across trials (a left/right item equally often required a response with the left or the right hand), we were able to independently characterize the selection of both attributes in the trial-average (thus circumventing any correspondence between our visual and motor selection signatures due to sheer volume conduction/signal mixing). We thus attribute lateralized patterns of neural activity that depend on item location (a purely visual attribute in our task) to visual selection and lateralized patterns that depend on required response hand to motor selection (followed by action implementation).

Two sets of complementary analyses converged on the notion of concurrent visual and motor selection during working-memory utilization.

We first focused on hypothesized spectral modulations in selected visual and motor electrode clusters (Methods for details). Figure 2a shows the time- and frequency-resolved neural modulation relative to the probed item’s location in visual electrodes. Visual selection was associated with a marked attenuation of 8–12 Hz alpha oscillations in electrodes contralateral (relative to ipsilateral) to the location of the probed item (Fig. 2a; cluster \( P < 0.0001 \); see Methods for details). This modulation occurred at posterior electrodes (Fig. 2b) and localized to visual and parietal brain areas (Fig. 2c). This agrees with previous reports of alpha attenuation during shifts of spatial attention in perception12, working memory (reviewed in ref.13) and long-term memory14, although we are not aware this has been demonstrated during working memory utilization. It is noteworthy that alpha lateralization reflecting selection

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Fig. 1 | Task, performance and hypothetical scenarios. a, Participants saw two colored bars and reproduced the tilt of the color-matching item after a working memory delay. Bar tilt was directly linked to the required response hand, such that a leftward (or rightward)-tilted bar required a reproduction response with the left (or right) index finger (see Methods for details). Each trial contained one leftward-tilted and one rightward-tilted bar, randomly allocated to the left and right positions on the screen, rendering item location and required response hand orthogonal across trials. b, Average response density (proportion of responses) as a function of the reported tilt and the tilt of the probed item. Zero degrees denotes vertical and negative (or positive) values denote a leftward (or rightward) tilt. c, Density of response deviation from the required tilt. Gray lines show individual participants, while the blue line shows the group average. d, Average density of response initiation times. Same conventions as in panel c. e–g, Hypothetical patterns of visual and motor selection after the memory probe. Shadings in panels b–d represent ±1 s.e.m., calculated across participants (n = 25).
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The spatial location of the probed item occurred despite item location not being strictly necessary for task performance (see also refs. 15,16). This ties in well with recent evidence that spatial location may play a grounding role for working-memory representations15,16. Provided that spatial location was a purely visual feature (as well as alpha modulations) in a re-analysis of our prior work8,19, the expected 13–30 Hz beta band emerged before response initiation (Supplementary Figs. 2 and 3). As shown in Fig. 3b, item-location information started in postresponse time (as opposed to induced) neural activity. Figure 3a shows that we could robustly decode both item location (cluster-P < 0.0001) and response hand (cluster-P < 0.0001) starting around 200 ms after probe onset (well before response initiation; see Fig. 1d, and equivalent results were observed for a number of decoding metrics, and Supplementary Fig. 4). To track the spatial-temporal trajectories of neural information linked to item-location and response-hand selection, we also applied this analysis iteratively for subsets of electrodes and source parcels in a searchlight fashion (as in refs. 22,23). As shown in Fig. 3b, item-location information started in posterior (putative visual) electrodes and soon spread out more widely. Motor information also spread out with time, but remained most prominent in central (putative motor) electrodes. A source analysis substantiated the respective contributions of visual and motor brain areas for initial item-location and response-hand decoding (Fig. 3c,d). This corroborates the independent nature of our visual and motor decoders (given that item location and response hand were orthogonally manipulated). A cross-generalization analysis, in which decoding of item location generalized between left and right response hand trials and in which decoding of response hand generalized between left and right item location trials (Supplementary Fig. 5), further reinforced the unique ability of our design and analysis to measure visual and motor selection effectively and independently. Moreover, we found highly similar decoding of the item location (as well as alpha modulations) in a re-analysis of our prior work8,19.

Fig. 2 | Spectral signatures of visual and motor selection during working memory utilization. a, Spectral lateralization (contralateral minus ipsilateral) in selected visual electrodes relative to the memorized location of the probed item. The black outline indicates the significant cluster (two-sided cluster-based permutation test; n = 25). Zero permutations yielded a larger cluster than in the observed data, yielding P < 0.0001 (provided 10,000 permutations). b, Topography of the difference in 8–12 Hz alpha power in the 400–800 ms interval between trials in which the memory probe prompted the selection of the left or right item in memory (left minus right). Note that the probe itself was always central. c, Source-level contrast equivalent to the sensor-level contrast in b. For visualization, only values at least 25% of the maximum/minimum value are displayed. d, Same conventions as in a, except lateralization was calculated relative to the response hand associated with the probed item and is displayed for the selected motor electrodes. Cluster-P < 0.0001, following 10,000 permutations. See Supplementary Fig. 1 for the complementary motor lateralization in selected visual electrodes and for visual lateralization in selected motor electrodes. e–f, Same conventions as in b and c, except data were contrasted for 13–30 Hz beta power between left and right response hands. The depicted item-location and response-hand contrasts were orthogonal. Results in all panels depict the average across all participants (n = 25).
dataset in which participants performed a similar visual working-memory task, but always responded with the same, dominant hand (Supplementary Fig. 6).

Thus, when memoranda in working memory have both visual and motor attributes, utilization involves selection of both types of attribute, engaging visual and motor brain areas at highly similar intervals after the memory probe. To reveal the temporal relation between visual and motor selection with greater granularity, we reduced the visual and motor spectral lateralizations to simple time courses and normalized all relevant time courses (for the spectral and the decoding signatures) to their peak value. This confirmed highly overlapping temporal profiles of visual and motor selection, and this was the case for both types of identified neural signature (Fig. 4a). The results showed no systematic lag indicative of a serial pattern of visual-then-motor selection. If anything, motor selection appeared to start even earlier than visual selection in the spectral signatures (although we note this slight temporal offset disappeared when aligning the data to response initiation; see Supplementary Fig. 3).

It is conceivable that the observed temporal correspondence at the group-average time courses was merely a coincidence, resulting from averaging slow participants who mainly showed the visual selection signatures with fast participants who mainly showed the motor selection signatures. To rule out this interpretation, we also used a complementary visualization of the temporal correspondence by calculating cross-correlations between the time courses of visual and motor selection per participant and averaging the resulting coefficients. This confirmed maximal correlations at approximately zero-lag in the vast majority of participants, as well as in their average (Fig. 4b). Another possibility is that some items (or some trials) engage a predominant visual memory code, whereas others a predominant motor code. Under this account, one may expect that responses would be faster following probes of motor-coded versus visually coded items and hence that faster trials would appear like the only motor scenario, whereas the slower trials would look more like the visual-then-motor scenario. Yet, we found that the concurrent nature of visual and motor selection was largely invariant to response onset time, with both selection signatures scaling similarly with response times (Supplementary Fig. 7a,b).

As a bonus, this analysis revealed that faster trials were characterized by neural lateralization patterns that favored the subsequently probed item, in line with the notion of a ‘spontaneous’ prioritization (‘pre-selection’) of that item (Supplementary Fig. 7c). This was the case for the spontaneous prioritization of the item’s visual location (lower contra versus ipsilateral alpha power in visual sites; a replication of ref. 15)—further arguing against the ‘only motor’ scenario, as well as its associated action (lower contra versus ipsilateral beta power in motor sites relative to the response hand associated with the probed item)—placing the motor contribution to visual working memory utilization also into the delay period.

To quantify the timings of visual and motor selection more formally, we applied a jack-knife approach to obtain temporal confidence intervals (as in refs. 22,25). Figure 4c shows the relevant 95% confidence intervals sampled from 10 to 90% of the identified peak
value in each time course. For comparison, the red points depict the predicted timings of motor selection under a strict serial model (Fig. 1e) in which motor selection starts when visual selection peaks. Clearly, the observed motor selection signatures occurred much earlier than predicted from this serial model. When expressed in t values (Fig. 4d), the observed motor selection time courses occurred highly significantly earlier than predicted by the serial null model (red points in Fig. 4d; average statistic across all of the ‘percentage-of-peak’ slices for the spectral data: $t_{np}(24) = -10.871$, $p_{np} = 2.13e-8$), whereas the timing of motor selection was never significantly later than predicted by the parallel null model (black points in Fig. 4d; average statistic for spectral data: $t_{np}(24) = -1.68$, $p_{np} = 0.175$; decoding data: $t_{np}(24) = 0.493$, $p_{np} = 0.648$).

Of course, it is impossible to rule out all viable ‘in-between’ models in which visual and motor selection are only slightly offset in time. However, if present, such delays are minimal compared to the time over which the neural signatures of visual selection evolve. Thus, even if visual and motor selection are not initiated in perfect synchrony, they clearly overlap during their operation, yielding concurrent availability of selected visual and motor attributes to guide performance.

Discussion

While memories inherently regard the past, the purpose of holding detailed sensory information available in memory is to guide adaptive future behavior. In this light, it is surprising that popular laboratory tasks of working memory have tended to consider visual and motor representations in isolation. Although we have gained a vast body of knowledge about working memory from studies that have focused primarily on visual or motor contents of working memory, our data make clear that the brain's natural tendency may be to link prospective manual actions to particular sensory representations during working memory. Thus, unlike in perception—in which sensory analysis necessarily precedes action selection—once sensory information has been encoded into working memory, the brain no longer needs to wait for the relevant sensory representation to be selected before considering the appropriate action. This
sensory-motor conceptualization of working memory may also account for the observation of similar capacity limits for visual working memory and action planning.

Previous empirical and theoretical work have suggested that the brain continuously specifies multiple potential actions in parallel before selecting among them. Our data suggest that such parallel action specification may also occur for the contents of ‘visual’ working memory and incorporate visual representations. Concurrent availability of both visual and motor memory attributes allows refinement of selected actions by detailed visual memory content, yielding action implementation that is both fast (compared to the visual-then-motor scenario) and precise (compared to the only motor scenario).

The current work uniquely targeted the selection of memories from their putative stores in visual and motor brain areas. Complementary research has posited a key role for frontal-striatal circuits in controlling the selection of information from working memory. Whether sensory and motor attributes of memories are jointly or independently represented in these ‘control circuits’, and how these circuits interact with the traces in the sensory and motor areas that we studied remain exciting avenues for future research.

The sensory-motor conceptualization of working memory promoted by the current work complements, and is to be distinguished from, prior work implicating a role for the brain’s oculomotor system in visual/spatial working memory, a role that is probably mediated by the involvement of this system in covert spatial attention. While oculomotor-driven attention mechanisms may also contribute to our visual selection signatures (as these depend on the spatial location of the probed memory item), our study uniquely also targeted the process of guiding a manual action by the memorized shape of the selected memory item (independently of its location). In this light, our data are thus compatible with the concurrent co-activation of two computations that may each be sensory-motor in nature, one dealing with the selection of the relevant visual shape information through its memorized location and the other dealing with the use of this information for guiding manual action.

In everyday situations, memorized visual information often guides action, such as when navigating to one’s bed after turning off the lights, or when changing lanes after having scanned surrounding traffic. To target the essential elements of how visual working memory guides action, we developed a laboratory task with relatively simple visual stimuli and actions. This enabled us to measure visual memory-guided action with high precision, and to track the dynamics of visual and motor selection independently in the EEG. As such, we believe our task and results provide an important step toward bridging the literature on visual working memory and action planning. Still, we only tested the relative timing of selecting a narrow set of visual attributes and motor responses. It will be important for future studies to address the generalizability of the current findings to different types of visual stimuli and action, and to start exploring the links between visual working memory and action in more naturalistic situations.

We finally note that the construct of working memory serves as a central component in many theories of cognitive and brain function, as well as dysfunction. The success and reach of such theories, and of related cognitive therapeutic interventions, will ultimately depend on the validity and breadth of our understanding of working memory. Our data highlight the importance of considering its fundamentally prospective, goal-oriented, nature for which the efficacy of utilization may be at least as important as the much more commonly considered capacity of retention.

Accession codes. All data are publically available through the Dryad Digital Repository: https://doi.org/10.5061/dryad.sk8rb66.

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Author contributions
F.v.E. designed and programmed the experiment, acquired, analyzed and interpreted the data and drafted and revised the manuscript. S.R.C. acquired and interpreted the data. M.G.S. interpreted the data and drafted and revised the manuscript. A.C.N. designed the experiment, interpreted the data, and drafted and revised the manuscript.

Competing interests
The authors declare no competing interests.

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Methods. This study complied with all relevant ethical regulations and was conducted in accordance with the declaration of Helsinki. Prior to the study, experimental procedures were reviewed and approved by the Central University Research Ethics Committee of the University of Oxford. Each participant provided written consent before participation and was reimbursed £15 per hour.

Participants. Twenty-five healthy human volunteers (11 male; age range 19–36; mean age 25.12 years) participated in the study. No statistical methods were used to pre-determine sample sizes but our sample size is similar to those reported in previous publications from the lab that focused on similar neural signatures (for example, ref. 16). All participants had normal or corrected-to-normal vision. Two participants were left-handed. Data from all participants were retained in the presented analysis.

Stimuli, task and procedure. Participants sat in front of a monitor (100-Hz refresh rate) at a viewing distance of approximately 95 cm. Each trial (Fig. 1a for a schematic) contained two peripheral oriented bars. One bar was always placed to the left and the other to the right of the central fixation cross, and one bar was tilted leftward and the other rightward. Across trials, bar tilt was orthogonal to bar location—that is, the left (right) position was equally often contained a leftward or a rightward tilted bar. Bars were centered at a viewing distance of 5.7° visual angle, and were 5.7° in length and 0.8° in width. Bars were randomly tilted between 20 and 70° (thus avoiding all tilts within 20° from vertical and horizontal). Unlike tilt direction, tilt magnitude was drawn independently between both items. In each trial, bars were randomly located two unique items out of a set of eight colors (RGB: 21, 165, 234), orange (RGB: 234, 74, 21), green (RGB: 133, 194, 18) and purple (RGB: 197, 21, 234). Colors were drawn independently of bar location and tilt.

Bars were displayed for 250 ms and followed by a working-memory delay (randomly drawn between 2,000 and 2,500 ms) during which only the fixation cross remained on the screen. After the memory delay, the central fixation cross changed into the color of either item (the memory probe). Until then, both items were equally probable to be probed. Participants were instructed to reproduce the tilt of the color-matching item as accurately as possible. For reproduction, participants used the ‘\’ (backslash) and ‘/’ (forward slash) keys on the keyboard, respectively, using their left and right index finger. Time between probe onset and response initiation was unlimited. On response initiation (with either key), a visual response dial appeared on the screen that always started in vertical position (indicated by the north and south handles of the dial, Fig. 1a). The response dial had the same diameter as the length of the visual bars and was always presented around fixation. A key press of the right (left) index finger initiated a clockwise (counter-clockwise) rotation of this dial, at the speed of 8 ms per degree (thus requiring 800 ms to bring the dial from vertical to horizontal). Participants were instructed to release the key when the dial arrived to the desired tilt. Only one key could be used per response and key release terminated the response (no adjustments could be made). The dial could not be rotated beyond ±90°, as the response would be terminated by the computer program. As a consequence, a leftward (rightward) tilted bar feedback could only ever be reported with a left (right) key press. Bar tilt was thus directly linked to the action that would be required if that bar would be probed. Visual feedback of the dial was included merely to aid participants’ performance in reporting the memorized visual orientation. Dial-feedback was independent of the visual memory attribute that we focused on pertaining to the memorized location of the probed item.

Because bar tilt and bar location were independent across trials, the location of each item was orthogonal (across trials) to the location (response hand) of its associated action. This key feature of our task allowed us to independently track neural activity related to the probed item’s memorized location (the visual attribute of interest) and the response hand associated with this item (the motor attribute of interest), while bypassing the contribution of sheer volume conduction/signal mixing.

Participants received feedback immediately after response termination. The fixation cross turned green for 200 ms for reports within 20° of the correct tilt, red otherwise. The inter-trial-interval (from feedback offset to encoding onset) was randomly drawn between 500 and 800 ms.

Participants practiced the task for 5–10 minutes until they reported being comfortable with it. They then completed two consecutive sessions of 1 hour with a 15 minute break in between. Each session contained 10 blocks of 60 trials, yielding 1,200 trials per participant. The location and the tilt (response hand) of the probed item were pseudo-randomized at the level of trials. This ensured that each condition (probed item left, left tilt; item left, right tilt; item right, left tilt; item right, right tilt) occurred equally often in each block of 60 trials. A visual localizer was inserted between blocks during which participants were asked to relax while keeping fixation. Each localizer contained 40 bars (identical to the ones used in the task) that were sequentially presented for 100 ms at an inter-stimulus-interval randomly drawn between 400 and 500 ms. Each localizer stimulus was randomly allocated one of the four colors, randomly tilted, and randomly presented at the left or right item position.

Data collection and analysis were not performed blind to the conditions of the experiments.

Analysis of behavioral data. We quantified accuracy as the average absolute circular deviation between the probed item’s tilt and the reported tilt, and response time as the interval between probe onset and response initiation. Only trials in which response initiation times were within 4 s.d. of the mean were considered. Response densities were quantified in bins of 10°, sampled in steps of 5° from 90 to +90 degrees. We separately considered items whose tilt fell between non-overlapping bins of 10° (that is, (−70 to −60), (−60 to −50), and so on). Response-time densities were quantified using 50-ms bins, sampled in steps of 25 ms from 0 to 1,250 ms.

EEG acquisition and basic processing. EEG was acquired using Synamps amplifiers and Neuroscan acquisition software (Compumedics Neuroscan). We used a 61-channel set-up that followed the international 10–10 system for electrode placement. Data were referenced to the left mastoid during recording and re-referenced offline to the average of both mastoids. The ground was placed on the left upper arm. Two bipolar electrode pairs recorded electrooculography: one above and below the left eye (vertical electrooculography) and another lateral of each eye (horizontal electrooculography). During acquisition, data were filtered between 0.1 and 200 Hz, digitized at 1,000 Hz and stored for offline analysis.

Data were analyzed in M/AMathWorks (Natick, MA) and FieldTrip44 and custom code. Data were down-sampled to 250 Hz and epochs relative to probe onset (from −1,500 to +2,500 ms) as well as response onset (from −2,500 to +1,000 ms). Ocular artifacts were removed from the data using independent component analysis (ICA). Relevant ICA components were detected through correlation with the horizontal and vertical electrooculography. For sensor-level analysis, we applied a surface Laplacian transform to increase spatial resolution.

We only considered trials in which participants pressed the correct key (which was the case in 92.07 ± 1.11 (M ± s.e.m.)% of all trials) and in which response times were within 4 s.d. of the mean. Remaining trials with excessive EEG variance were rejected on the basis of visual inspection. For example, it was possible that trials in which item location and response hand were associated with the same or opposite side had become slightly over-represented in the data. To re-balance the data, we finally made sure that item location and required response hand were equally often in the same or the opposite side. Trial numbers were equated by randomly subsampling from the case with more trials. On average, 955 ± 25 (M ± s.e.m.) trials (ranging between 710 and 1,144) were retained for analysis per participant.

Spectral analysis. Time-frequency analysis was based on a short-time Fourier transform of Hanning-windowed data. We estimated spectral power at frequencies between 2 and 50 Hz in 1-Hz steps, using a fixed 300-ms sliding time window that was advanced over the data in 10-ms steps. To zoom in on localized modulations in visual and motor electrodes, we contrasted time-frequency matrices in selected visual and motor electrode clusters between trials in which either the item or the response location was contra-ipsilateral to the electrode cluster. We expressed this as a normalized difference (that is, (contra-ipsi) / (contra + ipsi)) × 100 and averaged the result between left and right electrode clusters. We did this separately for the visual and motor electrode clusters. To obtain topographical maps of lateralization, we also calculated separately for each electrode the normalized difference between left versus right item location as well as left versus right response hand.

For each participant, we determined four electrode clusters: left visual, right visual, left motor, right motor. Visual clusters were defined by contrasting the neural response induced by left versus right visual stimuli that were part of a task-free localizer. Motor electrodes were selected on the basis of the neural response locked to all left versus right button presses. Per cluster, we always selected between two and four electrodes on the basis of visual inspection of the data at this selection stage. Although the use of participant-specific electrode selections increases sensitivity, our results are not contingent on this selection; equivalent results were obtained when using a generic set of a priori defined electrodes (PO7 for left visual, PO8 for right visual, C3 for left motor, C4 for right motor).

To reduce time-frequency noise by applying a low-pass filter with a 30-Hz cut-off. Broadband (0.1–30 Hz) evoked responses for which we applied two additional multivariate decoding analysis. Multivariate decoding was based on the fieldtrip package of the open-source software FieldTrip44 and custom code. Relevant ICA components were defined 8–12-Hz alpha band for the item-location lateralization in the visual electrode clusters and we averaged over the a-priori defined 8–12-Hz alpha band for the item-location lateralization in the visual electrode clusters and we averaged over the a-priori defined 13–30-Hz beta band for the response-hand lateralization in the motor electrode clusters.

Multivariate decoding analysis. Multivariate decoding was based on the broadband (0.1–30 Hz) evoked responses for which we applied two additional pre-processing steps that are conventional in the analysis of evoked activity: we subtracted a trial-specific 250 ms pre-probe baseline and we removed high-frequency noise by applying a low-pass filter with a 30-Hz cut-off.

Decoding was evaluated separately for each time sample and was based on the multivariate Mahalanobis distance metric in which each several dimensions (as in refs. 21,22). Decoding relied on a leave-one-out procedure. For each trial, we calculated the Mahalanobis distance between that trial and the average of all remaining trials whose class was either matching or non-matching with the trial under investigation. Classes were defined once by matching/non-matching item location (yielding item-location decoding) and once by matching/non-matching item orientation (yielding item-orientation decoding). The decoding was evaluated using a classification criterion: the total correct classification probability (i.e. the probability of correctly classifying the trial as either matching or non-matching). To further quantify decoding performance, we calculated the multivariate decoding accuracy (MDA) as the percentage of trials correctly classified. To estimate the false alarm rate, we calculated the proportion of trials for which decoding accuracy was higher than chance level, which was defined as the proportion of trials for which MDA was higher than the proportion of decoding accuracy that would be expected by chance alone. To determine the significance level for our decoding results, we used the bootstrap method to generate a null distribution of decoding accuracy and to estimate the standard error of the proportion of trials for which decoding accuracy was higher than chance level. Finally, we used a mixed-effects repeated-measures analysis of variance (ANOVA) to test whether MDA was modulated by item location, response hand, or their interaction. The only factor that was found to significantly affect MDA was item location, with a contrasts contrast test showing that left visual items were associated with higher MDA compared to right visual items. The interaction between item location and response hand was also significant, with a contrasts contrast test showing that left visual items were associated with higher MDA when matched to the left response hand compared to when matched to the right response hand.
response hand (yielding response-hand decoding). If the multivariate neural pattern contains information regarding the class under consideration, then the multivariate distances should be smaller to the average of the matching class compared to the non-matching class. To express decoding as a positive value, we therefore subtracted the non-matching from the matching distances and averaged this metric across trials.

To maximize sensitivity, our main decoding analysis was based on all 61 EEG electrodes. We additionally performed this analysis iteratively for subsets of electrodes to obtain decoding topographies (as in refs. 19,20). In each iteration, we centered our ‘searchlight’ on a different electrode that we considered together with its immediately adjacent lateral neighbor(s), yielding subsets of two electrodes for all ‘outer’ electrodes, and subsets of three for all ‘inner’ electrodes.

To increase sensitivity and visualization, we lightly smoothed the trial-averaged decoding time courses for each participant using as Gaussian kernel with a standard deviation of 20 ms. We confirmed that this step was not essential and that qualitatively similar (albeit slightly more noisy) results were obtained when no smoothing was applied.

**Source analysis.** We placed a grid with 1-cm² spacing inside the generic MNI T1 template brain and used a boundary-element volume-conduction model21 to describe how activity in each grid point projected to the electrodes positioned according to the generic 10-20 system. Before source analysis, data were re-referenced to a common average reference.

Spectral power was localized using a frequency-domain beamformer22. For each grid point, we calculated the normalized difference in power between trials in which the item/response hand was on the left versus right in the same way as we had done at the sensor-level. Separate analyses were run for the α (~8–12 Hz) alpha band and the β (~13–30 Hz) beta band.

To evaluate decoding at the source level, we applied a time-domain beamformer23 to obtain three spatial filters associated with each grid point. We then used the anatomical automatic labeling atlas to allocate every spatial filter to its corresponding source parcel. To reduce dimensionality, for each parcel, we entered all allocated spatial filters to a singular value decomposition and retained the five components (spatial filters) with the largest singular value. These components were used to re-construct five virtual channels per parcel, the time courses of which were entered into our multivariate decoding analysis, yielding the identified patterns49 and were not subjected to further statistical evaluation. We also obtained confidence intervals for the temporal offset between the time courses of visual and motor selection (motor minus visual). Comparing this offset to 0 entailed a test against the parallel null model. A test against the serial null model was provided by the comparison of this offset to the predicted temporal shift if motor selection would start when visual selection peaked. This shift was determined by the start-to-peak (that is, 10–100%) duration of the visual selection time course. Effectively, we thus compared the motor selection time course once to the visual selection time course as observed, and once to this time course shifted by its own duration.

All reported measures of spread involve ±1 s.e.m., calculated across participants (n=25). All inferences were two-sided at an alpha level of 0.05 (0.025 per side). Data distributions were assumed to be normal but this was not formally tested. We report a single experiment with 25 participants that was not repeated.

**Statistical analysis and latency quantification.** Statistical analysis involved two steps: (1) evaluating the identified neural signatures of visual and motor selection and (2) quantifying their temporal relationship.

For step 1, we used a cluster-based permutation approach24 that is ideally suited for evaluating the reliability of neural patterns at multiple neighboring data points, as in our case along the dimensions of time and (for the spectral analysis) frequency. This approach effectively circumvents the multiple-comparisons problem by evaluating clusters in the observed group-level data against a single permutation distribution of the largest clusters that are found after random permutations (or sign-flipping) of the trial-average data at the participant-level. We used 10,000 permutations and used Fieldtrip’s default cluster-settings (grouping adjacent same-signed data points that were significant in a mass univariate t-test at a two-sided alpha level of 0.05, and defining cluster-size as the sum of all t values in a cluster). The P value for each cluster in the non-permutated data is calculated as the proportion of permutations for which the size of the largest cluster is larger than the size of the considered cluster in the non-permutated data. When zero permutations yield a larger cluster (as was the case for all our analyses), this Monte Carlo P value is thus smaller than 1/N permutations (in our case P < 0.0001).

We applied this approach to the time-frequency maps and to the decoding time courses. Topographical and source analyses served only to verify the plausibility of the identified patterns25 and were not subjected to further statistical evaluation.

Step 2 involved two analyses. First, we calculated cross-correlation coefficients (using the xcov function in MATLAB) between the identified time courses of visual and motor selection. We did this separately for each participant and averaged the resulting coefficients. The main purpose of this complementary visualization of the data was to rule out that the temporal relations observed at the group-level may not be representative because different participants may drive the timing of the different time courses. Second, we used a jack-knife approach to obtain temporal confidence intervals (as in refs. 26,27). To increase transparency and avoid the arbitrary selection of a particular aspect of each time course (its onset, peak, midpoint, point, and so on), we always considered several ‘slices’ of each time course, ranging from 10% of the peak value to 90% of the peak value in steps of 10%. For the jack-knife quantification, we iteratively removed one participant from the participant pool and, for each slice, compared the time at which that slice-value first occurred to the time that was observed when all participants were included. The jack-knife-based estimate of the temporal standard error then allowed us to obtain 95% confidence intervals under the Student’s t-distribution28. We also obtained confidence intervals for the temporal offset between the time courses of visual and motor selection (motor minus visual). Comparing this offset to 0 entailed a test against the parallel null model. A test against the serial null model was provided by the comparison of this offset to the predicted temporal shift if motor selection would start when visual selection peaked. This shift was determined by the start-to-peak (that is, 10–100%) duration of the visual selection time course. Effectively, we thus compared the motor selection time course once to the visual selection time course as observed, and once to this time course shifted by its own duration.

All reported measures of spread involve ±1 s.e.m., calculated across participants (n=25). All inferences were two-sided at an alpha level of 0.05 (0.025 per side). Data distributions were assumed to be normal but this was not formally tested. We report a single experiment with 25 participants that was not repeated.

**Code availability**

Code will be made available by the authors upon reasonable request.

**Data availability**

All data are publicly available through the Dryad Digital Repository at: https://doi.org/10.5061/dryad.sk8rb66.

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- Clearly defined error bars
  - *State explicitly what error bars represent (e.g. SD, SE, CI)*

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| Data collection | Neurobs Presentation version 18.3 07.18.16 |
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|                 | Neuroscan SCAN version 4.5               |

| Data analysis   | FieldTrip version 20151213               |
|-----------------|------------------------------------------|
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Life sciences study design

All studies must disclose on these points even when the disclosure is negative.

**Sample size**
- Twenty-five healthy human volunteers (11 male; age range 19-36; mean age 25.12 years) participated in the study. No statistical methods were used to pre-determine sample sizes but our sample size is similar to those reported in previous publications from the lab that focused on similar neural signatures (e.g. ref 16).

**Data exclusions**
- Data from all participants were retained for analysis. At the level of trials, we only considered trials in which participants pressed the correct key (which was the case in 92.07 ± 1.11 [M ± SE] % of all trials) and in which response times were within 4 SD of the mean. Remaining trials with excessive EEG variance were rejected based on visual inspection. After trial removal, it was possible that trials in which item location and response hand were associated with the same or opposite side had become slightly over-represented in the data. To re-balance the data, we finally made sure that item location and required response hand were equally often in the same or the opposite side. Trial numbers were equated by randomly subsampling from the case with more trials. On average, 955 ± 25 (M ± SE) trials (ranging between 710 and 1114) were retained for analysis per participant (out of 1200 in total). The exact values for exclusion were not pre-established. Apart from the re-balancing procedure described above, trial exclusions were always performed while considering all trials; without knowledge of the experimental condition to which individual trials belonged.

**Replication**
- No replication was attempted as the primary results were all highly reliable.

**Randomization**
- The location and the tilt (response hand) of the probed item were pseudo-randomised at the level of trials. This ensured that each condition (probed item left, tilt left; item left, tilt right; item right, tilt left; item right, tilt right) occurred equally often in each block of 60 trials. There were no experimental groups to randomize, as this was a within-subjects design.

**Blinding**
- Data collection and analysis were not performed blind to the conditions of the experiments. Because there were no experimental groups, blinding was not relevant.

Reporting for specific materials, systems and methods

**Materials & experimental systems**

| n/a | Involved in the study |
|-----|-----------------------|
| ❑   | Unique biological materials |
| ❑   | Antibodies |
| ❑   | Eukaryotic cell lines |
| ❑   | Palaeontology |
| ❑   | Animals and other organisms |
| ❑   | Human research participants |

**Methods**

| n/a | Involved in the study |
|-----|-----------------------|
| ❑   | ChIP-seq |
| ❑   | Flow cytometry |
| ❑   | MRI-based neuroimaging |

**Human research participants**

Policy information about studies involving human research participants

**Population characteristics**
- Twenty-five healthy human volunteers (11 male; age range 19-36; mean age 25.12 years) participated in the study. All participants had normal or corrected-to-normal vision. Two participants were left handed. Nearly all participants were undergraduate students at the University of Oxford or at Brookes University. Because this was a within-subjects design, none of these variables constituted a relevant co-variate.

**Recruitment**
- Participants were recruited through flyers and an online participant database (SONA) at the University of Oxford. There was no selection bias by the experimenters. The only potential ‘bias’ is that the vast majority of participants were university students (as is commonly the case in cognitive neuroscience studies).