Does aging impair the capacity to use stored visuospatial information or online visual control to guide reach-to-grasp reactions evoked by unpredictable balance perturbation?

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Running head: Visual control of compensatory grasping

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ABSTRACT

Background: Rapid reach-to-grasp reactions are a prevalent response to sudden loss of balance and play an important role in preventing falls. A previous study indicated that young-adults are able to guide functionally-effective grasping reactions using visuospatial information (VSI) stored in working memory. This study addressed whether healthy older-adults are also able to use “stored”-VSI in this manner, or are more dependent on “online” visual control.

Methods: Liquid-crystal goggles were used to force reliance on either stored or online-VSI while reaching to grasp a small handhold in response to unpredictable platform perturbations. A motor-driven device varied the handhold location unpredictably for each trial. Twelve healthy older-adults (65–79 years) were compared to twelve young-adults (19–29 years) tested in a previous study.

Results: Reach-to-grasp reactions were slower and more variable in older-adults, regardless of the nature of the available VSI. When forced to rely on stored-VSI, both age groups showed a reduction in reach accuracy; however, a tendency to undershoot the rail was exacerbated in the older-adults. Forced-reliance on online-VSI led to similar delays in both age groups; however, the older-adults were more likely to reach with the “wrong” limb (contralateral to the handhold) and/or raise both arms initially (possibly to “buy” more time for final limb-selection).

Conclusion: Situations that force the CNS to rely on either stored or online VSI tend to exacerbate age-related reductions in speed and accuracy of reach-to-grasp balance-recovery reactions. Further work is needed to determine if this increases risk of falling in daily life.
INTRODUCTION

Rapid reach-to-grasp reactions are often executed (in combination with reactions involving the lower-limb and axial musculature) to prevent falling in response to a sudden “loss of balance” perturbation (1-3). These compensatory (balance-recovery) reactions are especially important for older-adults because of their increased risk of falling and their increased tendency to use reach-to-grasp reactions to restore postural stability (4,5). To grasp an object, it is necessary to identify and locate a suitable handhold and to use this visuospatial information (VSI) to guide the reaching movement. Compensatory grasping, however, presents additional demands, as it is also necessary to adjust the reach trajectory so as to compensate for the ongoing perturbation-induced motion of the torso (6). Furthermore, the urgent need to react rapidly in order to prevent a fall imposes temporal constraints that may severely limit the capacity to acquire and process the needed VSI (4).

Studies of natural gaze behaviour suggest that the needed VSI may be acquired and stored automatically as a contingency, through natural exploratory gaze behavior, as the person moves about in his/her environment (5,7). This then allows the hand to be moved very rapidly toward the nearest available handhold, if and when an unexpected balance perturbation occurs. The ability to use stored-VSI to guide effective reach-to-grasp reactions is further demonstrated by studies in which liquid-crystal goggles were used to block vision at time of balance-perturbation onset (PO) (6,8). Results showed that healthy young-adults were almost always able to recover balance successfully by reaching to grasp a small handhold that changed position unpredictably prior to PO; however, forced reliance on stored-VSI did lead to a reduction in the accuracy of the arm movement and a tendency to undershoot the handhold slightly (8). Conversely, forced reliance on online-VSI (by occluding vision prior to PO) led to slowing of the
arm movement and delay in contacting the handhold, possibly to “buy” more time to acquire and process the needed VSI and to adjust the arm trajectory in-flight.

Although healthy young-adults were always able to achieve a functionally-adequate grasp despite the effects of the visual manipulations on the accuracy and speed of the arm movement (8), it is not clear whether older-persons are equally able to use either stored or online-VSI to guide their grasping reactions. For example, older-persons may be less able to accurately store and retrieve salient VSI due to declines in working spatial memory (9), leading to increased reliance on online visual control (10); however, the latter may be compromised due to age-related slowing of visual processing and associated slowing of reaction time and movement speed (11-13). This age-related slowing could exacerbate the slowing that was observed in young-adults when they were forced to rely on online-VSI (8), and could thereby jeopardize successful balance-recovery.

The objective of the present study was to determine if aging impairs the ability to use stored or online-VSI to guide effective reach-to-grasp balance-recovery reactions evoked by unpredictable balance perturbations. Liquid-crystal goggles were used to force healthy older-adults to rely on either stored or online-VSI in order to grasp a small handhold that changed position unpredictably prior to PO, and results were compared to our previous study in which healthy young-adults performed the same protocol (8). We hypothesized that the previously-reported effects (reduced accuracy when dependent on stored-VSI, slowing of motion when dependent on online-VSI) would be exacerbated in the older-adults, and that these effects would be accompanied by an increased frequency of overt motor errors (e.g. selecting the “wrong” arm, hand-handhold collision) and compromised balance-recovery (e.g. increased frequency of “falls” into a safety harness).
METHODS

Participants

Twelve naïve, community-dwelling healthy older-adult subjects [six male, six female; ages 65-79 years (mean=72); mass 52-96kg (mean=71); height 157-182cm (mean=168)] were tested and compared to twelve younger-adult subjects tested in the previous study [six male, six female; ages 19-29 years (mean=23); mass 48-86kg (mean=66); height 159-186cm (mean=172)] (8). All subjects were right-handed, and able to stand and walk without aid. Exclusion criteria included: a recent history of falls (one or more in last year); recurrent dizziness or feelings of imbalance or unsteadiness; diabetes, neurological or sensory disorders; use of medications that may affect balance; joint replacement; medical conditions interfering significantly with daily activities; or functional limitations of limb use. Subjects were required to have a minimum Mini-Mental-Status-Examination score of 24/30 and a minimum Snellen visual acuity of 20/40 (or 0.5) without spectacles. As indicated in Table 1, the older-adults tended to perform nearly as well as the young-adults on various cognitive and visual tests.

Each subject provided written informed consent to comply with ethics approval granted by the institutional review board. All subjects participated in a short and separate balance study involving three gait-perturbation trials (5,7) immediately prior to the start of the present study.

Protocol

The protocol was identical to the earlier study involving young-adults (8). Briefly, balance-recovery reach-to-grasp reactions were evoked by sudden forward (0.405m/s, 1.35m/s²) or backward (0.6m/s, 2m/s²) translation of a 2m×2m computer-controlled motion-platform (14). Analyses focused on grasping reactions evoked by forward platform translation (backward falling motion); however, to deter predictive or anticipatory responses, the protocol also included
backward platform translations (~30% of trials) and “catch” trials where the motion-platform did not move (~15% of trials).

At the start of each trial, subjects stood in a comfortable standardized stance (15), with arms at sides, and faced a small motor-driven handhold (16) which subsequently moved from the starting position (midline) to one of four locations (left or right of midline; distance from mid-sagittal plane=50% or 75% of shoulder-width); see Figure 1. PO was then triggered after a random delay of 2-5 s. Subjects were instructed to recover balance by grasping a red-tape-marked “target” section of the handhold (length=125% of hand-width) as quickly as possible after PO with an overhand grasp, using the hand closest to the target. Foam blocks surrounded the feet to deter subjects from stepping, and a safety harness prevented falls.

Three visual conditions were tested by using liquid-crystal goggles (17) to occlude vision: 1) from start-of-trial to PO (forced reliance on online-VSI), 2) from PO to end-of-trial (forced reliance on stored-VSI), or 3) not at all (normal-VSI). Goggle-translucency activation (stored-VSI trials) or de-activation (online-VSI trials) was synchronized with PO (platform acceleration >0.1 m/s^2) via computer control. For each visual condition, each subject performed two blocks of 14 trials. Each block comprised (in random order): two forward-translation trials at each of the four handhold positions, four backward-translation trials, and two ‘catch’ trials (no platform motion). Subjects were informed of the visual condition prior to starting each block. Order of the blocks was balanced across and within subjects. To dampen learning effects, five unrestricted-vision trials were performed at the start of the session, and seven additional practice trials (pseudorandomized perturbation direction and handhold location) were performed each time a new visual condition was introduced [the first and last practice trial always involved the same task conditions (forward platform translation, handhold 75% of shoulder-width to left of mid-line), to allow analysis of learning effects].
Data collection and analysis

Recordings from four video cameras were used to determine: which arm was used to grasp the handhold; whether a full grasp (“power grip”) was achieved (all digits wrapped around handhold); whether a collision error occurred (contact with back of wrist or hand); and whether the subject attempted to step (by kicking the foam barriers) or fell into the safety harness (confirmed by harness-cable load-cell). Surface-electrode electromyographic (EMG) signals (band-pass filtered 10-500Hz; sampling-rate=1000Hz) were used to determine reaction time, which was defined as the earliest onset latency (determined by computer algorithm and confirmed by visual inspection) in any of three reach-arm muscles (anterior deltoid, lateral deltoid, biceps). Force-sensing resistors on the handhold (sampling-rate=200Hz) were used to determine contact time, which was confirmed using the motion-analysis system described below (hand-velocity <5% of peak). Both reaction- and contact-time were defined relative to onset of platform acceleration (>0.1m/s²), recorded by an accelerometer. To characterize reach accuracy, kinematic data (sampling-rate=200Hz; low-pass filtered at 6Hz with a dual-pass fourth-order filter) were collected by a three-dimensional motion-analysis system (Vicon-Peak Performance; Englewood, CO) and used to determine the hand location (marker on third knuckle, relative to markers mounted at each end of the handhold) at time of handhold-contact.

Repeated-measures analysis-of-variance (ANOVA) and post-hoc Tukey multiple-comparisons were performed to test the hypotheses. The primary dependent variables were: 1) frequency of full-grasp, grasping with the “wrong” arm and hand-handhold collision; 2) reaction- and contact-time; 3) reach accuracy and variability (in each coordinate direction). The focus of the analyses was on effects due to age, visual-condition and age×vision interaction. Accordingly, to simplify the data presentation, we have reported mean values (and standard deviations) determined across all handhold locations. Nonetheless, in each ANOVA, handhold side (left or
right) and eccentricity (50% or 75% of shoulder-width from midline) were included as within-subject factors in order to account for variance related to handhold location. All data were rank-transformed prior to analysis to avoid errors arising from potential violations of the assumptions underlying the ANOVA (18). The criterion level of significance was 0.05.

For the frequency variables, the proportion of trials in which the event was observed was calculated within each subject, for each of the 12 experimental conditions (3 visual conditions x 4 handhold positions), and the ANOVA was performed on the rank-transformed proportions. To analyze accuracy variability, the standard deviation of the grasp error was determined within each subject, for each of the 12 experimental conditions, and the ANOVA was performed on the rank-transformed standard deviations. For all of the other variables, rank-transformed data from individual trials were used. Each subject performed 48 trials; therefore, there were a total of 576 trials potentially available for analysis, within each age group. Trials in which subjects may have initiated the “decision” to move the arm prior to perturbation onset (EMG latency <70ms, i.e. faster than previously-reported latencies (1)), failed to react rapidly to the perturbation (EMG latency >250ms, movement-time >550ms, or contact-time >750ms) or failed to reach for the rail were excluded (n=16 for young-adults, n=35 for older-adults).
RESULTS

Both young and older subjects were generally well able to react to the balance perturbation by grasping the handrail rapidly (as instructed) and to recover equilibrium. None of the subjects fell into the safety harness (maximum harness loading <5% body-weight) and stepping to recover balance (by kicking the foam barriers) occurred in only one (older-adult) trial. However, the older-adults were significantly more likely to sustain hand-handhold collision (3.1% of trials vs. 0.5% in young-adults; p=0.029). These collisions occurred in seven of the older-adults (1 of 48 trials in three subjects, 3-4 trials in four subjects). Older-adults also appeared to be somewhat less likely to achieve a full-grasp (mean frequency: 73% of trials, vs. 86% in young-adults; p=0.11), but this may have been due primarily to the low scores (0-25%) in two older-adults (versus 72-90% in the others).

There were a number of age-related differences in the timing and accuracy of the reach-to-grasp reactions, and in the extent to which the timing and accuracy were affected by the visual task conditions, as detailed below. In addition, the older-adults were more likely to select the “wrong” arm (contralateral to the handhold), which necessitated a longer reaching motion across the body (mean frequency: 3.0% of trials vs. 0.0% in young-adults; p=0.0015), particularly when dependent on online-VSI (mean frequency: 7.8% of trials vs. 1.2% of normal-VSI and 0.0% of stored-VSI trials; p=0.0007). Furthermore, older-adults were more likely to raise both hands (up to handhold height) prior to grasping the handhold with the “correct” arm (mean frequency: 13.5% of trials vs. 2.8% in young-adults; p=0.020). Again, this tendency was most pronounced in online-VSI trials (mean frequency: 20.1% of trials, vs. 12.7% of normal-VSI and 7.8% of stored-VSI trials within older-adults; 6.4%, vs. 2.1% and 0.0%, respectively, within young-adults; p=0.006). All but one older-adult raised both arms in one or more trials (1-3 trials in five subjects, 5-8 trials in four subjects, 13-22 trials in two subjects), whereas “wrong-arm” reaches
were limited to six older-adults (2-4 trials in each case).

In terms of timing (Figure 2), the mean EMG onset-latency (reaction time) was slower in older-adults (168ms vs. 155ms; p=0.035) and time-to-handhold-contact was delayed further (539ms vs. 509ms; p=0.029). Visual condition had a significant main effect (p’s<0.0001) for both reaction and contact time, but the effect was similar in both age groups (age×vision interaction: p=0.48 for reaction time, p=0.65 for contact time). Post-hoc analysis revealed that reaction times were faster when forced to rely on stored-VSI (149ms), compared to online-VSI (167ms) or normal-VSI (167ms). For contact time, responses were fastest in stored-VSI (506ms), slower in normal-VSI (522ms) and slowest in online-VSI trials (543ms).

Analysis of the systematic (mean) reach accuracy (Figure 3) showed no significant main effects due to age in the antero-posterior and medio-lateral directions (p’s>0.13), and only a small effect in the vertical direction (58mm for older-adults vs. 56mm for young-adults; p=0.015). There was, however, a significant effect due to visual-condition in all three coordinate directions (p’s<0.0001). Specifically, in stored-VSI trials, the hand tended to contact the handhold with lateral error (5.7mm vs. 0.0mm for normal-VSI and -6.8mm for online-VSI), antero-posterior undershoot (-41mm vs. -12mm for normal-VSI and -11mm for online-VSI) and reduced elevation (53mm vs. 59mm for normal-VSI and 59mm for online-VSI). A significant age×vision interaction (p=0.034) for antero-posterior error revealed that the tendency to undershoot the rail when dependent on stored-VSI was heightened in older-adults. There was no significant age×vision interaction in the medio-lateral (p=0.12) or vertical (p=0.70) directions.

Older-adults exhibited greater variability than young-adults (Figure 4) in medio-lateral (15.8mm vs. 13.3mm; p=0.0075) and antero-posterior (26.8mm vs. 22.6mm; p=0.037) hand-landing position; however, visual condition had no effect on medio-lateral (p=0.95) or antero-posterior (p=0.074) variability. Conversely, vertical variability was not significantly affected by
age (p=0.061), but was strongly affected by forced dependence on stored-VSI (9.0mm vs. 6.8mm for normal-VSI and 5.9mm for online-VSI; p=0.0001). There was no significant age×vision interaction for variable error in the vertical (p=0.18) and medio-lateral (p=0.54) directions; however, antero-posterior variability did exhibit this interaction (p=0.031). For older-adults, post-hoc analysis revealed that antero-posterior variability was significantly reduced in stored-VSI trials (21.6mm, vs. 30.0mm for normal-VSI and 28.7mm for online-VSI), whereas the young-adults showed no significant differences between visual conditions.

Analysis of learning effects (comparing the first and last of the seven practice trials performed prior to each new visual condition) revealed similar changes in reach accuracy in both age groups: mean lateral error decreased with practice by 16mm (p=0.011), with more pronounced decreases in stored- and online-VSI trials (32mm and 26mm, respectively, vs. 6mm in normal-VSI trials; vision×trial-number interaction p=0.0082), whereas mean antero-posterior undershoot increased with practice across all visual conditions (-2mm vs. -20mm; p=0.0093). The only other variable to show a significant learning effect was frequency of full-grasp, which improved with practice (across all visual conditions) in older-adults (28% of trials vs. 72%) but not in younger-adults (81% vs. 81%; age×trial-number interaction p=0.025).
DISCUSSION

Generally, the results showed that reach-to-grasp accuracy and timing were influenced in a similar manner in both age groups when subjects were forced to rely on either online- or stored-VSI, namely, mean end-point accuracy was reduced when dependent on stored-VSI and timing was delayed when dependent on online-VSI. Support for our hypothesis that these effects would be more pronounced in the older subjects is provided by the analysis of antero-posterior accuracy, where the older subjects showed a disproportionately greater tendency to undershoot the rail when forced to rely on stored-VSI. Furthermore, our hypothesis that these visual manipulations would lead to an increased frequency of overt motor errors in the older-adults is supported by the findings that these subjects were more likely to select the “wrong” arm when dependent on online-VSI. There was, however, no evidence to support our hypotheses that the visual manipulations would exacerbate age-related impairment in ability to grasp the handhold and recover equilibrium successfully.

An unexpected finding was that older-adults were much more likely than the young to raise both hands in response to the perturbation, prior to selecting which arm to use to grasp the handhold, especially during the online-VSI trials. This could possibly be an adaptive strategy that serves to “buy” time for the VSI-processing needed to select the most appropriate limb, without causing delay in initiating arm movement. Based on online-VSI acquired during the initial raising of the arms, the CNS could then terminate the motion of the “incorrect” (contralateral-to-handhold) arm and complete the reach with the “correct” (ipsilateral) arm. Further research is needed to determine whether a bilateral-arm-raise strategy can lead to faster handhold contact, and to explore other possibilities, e.g. that the raising of both arms served to help “counter-balance” the backward falling motion of the body (3).
The presently-observed tendency to undershoot targets when dependent on stored-VSI has also been reported to occur in young-adults in previous studies of volitional arm movements (19,20). It has been suggested that this may be a strategy to ensure that the hand does not collide with the target (in the absence of any opportunity for online visually-guided corrections to the reach trajectory) (19,20). The larger undershoot errors (and reduction in undershoot variability) that we observed in older-adults may possibly reflect a heightened concern about avoiding handhold collisions. Alternatively, the greater undershoot may reflect systematic age-related errors in encoding the spatial representation of the handhold location in working spatial memory and/or errors in retrieving the encoded information (20).

The failure to see the hypothesized exaggerated slowing of reactions in older-adults when dependent on online-VSI may be due, at least in part, to use of adaptive strategies by the older-adults to counter the slowing. As mentioned above, the strategy of raising both arms initially, which occurred almost entirely within the older subjects (11/12 vs. only 2/12 young-adults), may have possibly served to allow for fast initiation of the reaction while buying more time for online processing of VSI. Alternatively, in some trials subjects may have avoided slowing of the reaction by electing to pre-select (prior to PO) which arm to use to grasp the handhold. Such a strategy would then, of course, lead to the use of the “wrong” arm in some of the trials. “Wrong-arm” trials only occurred in the older-adults and occurred almost entirely in online-VSI trials.

It is not clear whether individuals would be able to use these adaptive strategies effectively in response to unexpected balance perturbations in daily life. If not, then the initiation of “real-life” reactions in older-persons when dependent on online visual control may actually be delayed to a greater extent than revealed in the present study. Since delays in handhold-contact time have been found to predict an increased risk of falling in daily life (21), any factors that increase the delay would be expected to further elevate fall risk. Thus, older-
adults could be at particularly high risk of falling in situations where they have failed to store accurate VSI about potential handhold locations proactively, e.g. when distracted while ambulating in an unfamiliar environment (5).

The difficulties that the older-adults appeared to experience under specific visual conditions were superimposed on general age-related impairments that were observed across all visual conditions. These impairments included a slowing of reaction time and contact time, increased variability in reach accuracy, and increased frequency of hand-handhold collision errors. Although, to our knowledge, no previous studies have analyzed age-related differences in the accuracy of perturbation-evoked reach-to-grasp reactions, age-related delays in the initiation and completion of such reactions have been demonstrated (21,22).

Despite the vision-dependent effects and age-related impairments revealed in this study, both young and older subjects were generally able to achieve a functionally-adequate grasp and prevent themselves from falling. This likely reflects the fact that the mean differences in reach timing and accuracy tended to be relatively small (~30ms or less and ~30mm or less). It remains to be determined whether these differences become larger, or have greater functional significance, when responding to larger perturbations. Our perturbation magnitudes were selected to be large enough to ensure that “feet-in-place” lower-limb postural reactions would be insufficient to recover equilibrium (and thereby necessitate grasping); however, we avoided using larger perturbations that might trigger stepping reactions in some trials and thereby confound analysis of the grasping reactions. Presumably, larger perturbations will require larger stabilizing hand-handhold reaction forces to be generated, and hence may require a stronger grip. Some of the “partial” grips that were sufficient to stabilize the body in the present study may prove to be inadequate in responding to larger perturbations; hence, grasp-accuracy demands may increase. In addition, larger perturbations will demand more rapid responses.
It is also possible that the effects observed in the present study may have greater functional significance when responding to unexpected balance perturbations in the complex environments and unpredictable situations of daily life. The fact that the experimental task conditions were limited to a finite number of options (two perturbation directions/magnitudes and four handhold locations) may have possibly allowed the CNS to encode motor commands for multiple trajectories/directions simultaneously prior to action selection (23); however, it is not clear the extent to which such “proactive” trajectory encoding is possible in situations where the perturbation-induced trunk motion is highly unpredictable. Instead, it has been suggested that stored VSI about potential handhold locations must be retrieved and combined with the online multi-sensory feedback arising from the perturbation-induced body motion in order to guide the hand to the handhold (7). Further work is needed to better understand the effects of aging on the visual control of perturbation-evoked reach-to-grasp in situations where the perturbation and handhold features are highly unpredictable, and to address the effects of concurrent cognitive or motor tasks.

Ultimately, this line of inquiry may lead to new cognitive-based interventions to improve control of balance reactions and reduce risk of falling. Recent studies support the potential for such interventions to improve balance and mobility in older-adults (24,25). We are currently exploring two approaches: 1) handrail-cueing systems to attract attention to the rail and facilitate encoding of rail location in spatial-working-memory, and 2) computer-based visual-training programs to improve ability to rapidly process VSI (26). The present findings suggest that it may be beneficial to also train spatial-working-memory and to augment perturbation-based training programs (27) with task conditions that increase reliance on either stored or online VSI.
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REFERENCES


Table 1. Visual and Cognitive Function.

<table>
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<th>Mean ± SD (minimum, maximum)</th>
<th>Comparative Data From Other Older Adult Studies†</th>
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<td>1.06 ± 0.31 (0.67, 1.54)</td>
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<td>Melbourne Edge test (dB)¶</td>
<td>23.9 ± 0.3 (23, 24)</td>
<td>23.2 ± 1.6 (19, 24)</td>
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<td>Depth perception</td>
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<td>Howard–Dolman test (cm)¶</td>
<td>0.98 ± 0.54 (0.28, 2.00)</td>
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<td>Useful field of view</td>
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<td>Subtest 1: speed of processing (ms)</td>
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<td>Cognitive function</td>
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<td>Mini-Mental Status Examination</td>
<td>Not tested</td>
<td>28.8 ± 1.27 (26.5, 30)</td>
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Note: *None of the differences between the two age groups were statistically significant (Student’s t test; p values > 0.097). Smaller scores indicate better test performance for all measures except for Snellen acuity test, Melbourne Edge test, and Mini-Mental Status Examination.
†All studies involved healthy community-dwelling older adults, except Lord and colleagues (14) used a combination of community-dwelling (n = 77) and nursing home residents (n = 79).
‡Expressed in Snellen decimal, for example, 20/40 = 0.5.
§SD was not reported.
¶dB: decibels (ranging from 1 = poor vision to 24 = good vision).
‖Error in matching positioning of rods.
#Subtests 1–3 correspond to stimulus-identification (speed of processing), divided-attention, and selective-attention tests.
** Determined during dual-task balance testing; SD was not reported.
Figure 1. Positioning of the moveable handhold on the motion platform. Dashed lines in the insert indicate the four handhold positions that were tested.
Figure 2. Effects of age and visual condition on reach-to-grasp timing: (a) reaction time; (b) handhold contact. Panel A displays the means (and standard deviations) for the young adults (unfilled bars) and the older adults (filled bars), as determined across all handhold locations. Panel B displays the means separately for each of the four handhold locations: left (L) or right (R) of midline, at a distance equal to 50% or 75% of shoulder width. § Indicates a significant difference due to age (main effect); * indicates significant differences due to visual condition (p < .05). Note the delay in contact time in online-VSI trials and the general age-related slowing across all visual conditions.
Figure 3. Effects of age and visual condition on reach-to-grasp accuracy, in each coordinate direction (format same as in Figure 2, except that † indicates differences in means associated with a significant Age × Visual condition interaction; $p < .05$). Positive values indicate systematic errors in the lateral, forward, and upward directions, respectively. Note the increased tendency for lateral error, reduced elevation, and anteroposterior undershoot in stored VSI trials, and the exacerbation of the latter effect in older adults.
Figure 4. Effects of age and visual condition on variability in reach-to-grasp accuracy (ie, standard deviation of the reach error, computed across repeated trials), in each coordinate direction (format same as in Figure 3). Note the reduced anteroposterior variability in stored VSI trials (relative to normal and online VSI) in the older adults, plus the age-related increase in mediolateral variability (across all visual conditions).