

Body position differentially influences responses to exogenous and endogenous cues

Jim McAuliffe · Michel J. Johnson · Bruce Weaver ·
Miranda Deller-Quinn · Steve Hansen

Published online: 4 October 2013
© Psychonomic Society, Inc. 2013

Abstract The influence of vestibular inputs on exogenous (Exp. 1) and endogenous (Exp. 2) orienting of visual attention was examined. The vestibular system was manipulated through a change in static body position. Participants engaged in an exogenous or endogenous response task while in a seated position, while lying in a prone position, and while in a prone position with their head down and neck flexed (HDNF). An attenuation of inhibition and facilitation effects during the exogenous task was observed in the HDNF position. However, responses to the cues remained similar in the endogenous task, irrespective of body position. The results reveal a potential dissociation between reflexive and volitional orienting of visual attention that is dependent on vestibular inputs.

Keywords Attention · Inhibition of return · Vestibular system

Many activities of daily living involve volitional and reflexive orienting of attention while the body is positioned in many orientations. Vestibular inputs play a major role in image stabilization during rotations and translations of the head (Raphan & Cohen, 2002) and during the regulation of the

translational vestibular ocular reflex (Seidman, Telford, & Paige, 1998), and are important for reflex mechanisms that help maintain upright posture by contributing to muscle tone in cats (Ishikawa & Miyazawa, 1980). A tilt of the head has also been shown to induce rotations of a produced figure during hand drawing (Guerraz, Boulin, & Vercher, 2003). Similarly, the orientation of the trunk relative to an impending target location and the direction that a person is walking can also affect our responses to visual information (Grubb, Reed, Bate, Garza, & Roberts, 2008). In addition, orienting the trunk toward the left visual field in people influenced by hemispatial neglect has been shown to compensate for performance deficits in saccadic reaction times (Karnath, Schenkel, & Fischer, 1991). In this context, our visual attention processes may operate differently when we are in different positions because of the change in vestibular inputs.

Research using the Posner cuing paradigm (e.g., Posner & Cohen, 1984) has typically been restricted to situations in which the participant is seated while viewing stimuli presented on a vertically oriented computer monitor. The cuing paradigm involves the central fixation of the visual display followed by the presentation of either an uninformative peripheral cue (i.e., exogenous) or a cue at the central fixation (i.e., endogenous) that can inform or misinform the participant of the impending target location (Posner & Cohen, 1984; Posner, Nissen, & Ogden, 1978). After a delay, a target is presented and participants respond by indicating that they detected it. The exogenous inhibition of return effect (IOR) is typically characterized by a slowing of response to a target that is presented in the same location as the cue if the stimulus onset asynchrony (SOA) is longer than 300 ms. Facilitation is typically observed for targets in the cued location if the SOA is less than 300 ms. The endogenous effect is characterized by shorter reaction time to targets preceded by valid indicators of the target location. These robust effects have been widely observed in multiple contexts (Spence, Lloyd, McGlone, Nicholls, & Driver, 2000; Taylor &

J. McAuliffe · S. Hansen
Nipissing University, North Bay, Ontario, Canada

M. J. Johnson
Université de Moncton, Québec, Québec, Canada

B. Weaver · M. Deller-Quinn
Lakehead University, Thunder Bay, Ontario, Canada

J. McAuliffe (✉)
Sensory–Movement Behaviour Lab, Physical and Health Education,
Nipissing University, 100 College Drive, North Bay, Ontario, Canada
P1B 8L7
e-mail: jimmc@nipissingu.ca

Klein, 1998). The two paradigms have been widely used to examine volitional (endogenous) and reflexive (exogenous) orienting of visual attention within a person (Kingstone & Pratt, 1999), during interpersonal interactions (Hayes, Hansen, & Elliott, 2010), and with special populations (Welsh, Ray, Weeks, Dewey, & Elliott, 2009). In this context, the purpose of our study was to examine the influence of body position on our capacity to respond to exogenous and endogenous visual cues.

Vestibular inputs were manipulated through a change in body position while participants completed either an exogenous (Exp. 1) or an endogenous (Exp. 2) cuing task. The participants were seated, lay prone with their head supported upright, or lay prone with their head down and neck flexed (HDNF) while they completed the task. Due to the stimulation of the otoliths in HDNF, tilting a person's head toward their trunk while they are lying prone evokes changes to neural-mediated blood flow responses (Essandoh, Duprez, & Shepherd, 1998; Shortt & Ray, 1997). While one is statically positioned in the HDNF orientation, the orientation of gravity relative to the head differs drastically from that of a typical head-upright position. Because a change in body orientation relative to potential target locations (Grubb et al., 2008; Karnath et al., 1991), changes in hand position relative to potential targets (Reed, Grubb, & Steele, 2006), and dynamic body maneuvers have all been shown to modify visual attention (e.g., Paige, Telford, Seidman, & Barnes, 1998; Seidman et al., 1998), it is entirely possible that the static HDNF position could influence visual attention. The combination of visual and vestibular inputs affects the current state of the system because the atypical positioning of the vestibular apparatus causes an increased demand on the multisensory processing that occurs within the central nervous system (Grubb et al., 2008). In this study, because of the static and continuous stimulation of the vestibular apparatus indicating an unusual orientation of gravity while in the HDNF position that would necessitate further multisensory integration (Angelaki, Gu, & DeAngelis, 2009; Stein & Stanford, 2008), participants were expected to experience less of an orienting response to the exogenous cue. In contrast, participants were expected to maintain their response to the endogenous cue due to the top-down mediation of visual attention (see Klein, 2000, for a review of IOR).

Experiment 1

Method

Participants A group of 15 undergraduates from Lakehead University were recruited. They ranged in age from 18 to 25 years, and all had normal or corrected-to-normal vision.

Apparatus All stimuli were presented on a standard computer monitor. A microswitch held in the participant's hand was used to record responses to the target stimuli. A cushioned table was used when the participants were requested to lie in the prone position. A head rest was used to fix the head in an upright position. The timing and presentation of the stimuli were controlled with a custom-made Superlab program (Cedrus Corporation, San Pedro, CA).

Task Participants responded to visual targets that were exogenously cued. Each trial began with a blank black screen (1,000 ms). Following that, a display consisting of the white outlines of two squares ($1^\circ \times 1^\circ$) located on the horizontal meridian 5° to the left and right of a central fixation dot (a filled white circle 0.2° in diameter) appeared for 1,000 ms. Subsequently, one of the boxes enlarged for 50 ms. Enlarging the exterior of the box to 1.1° made the box appear to brighten. The original two squares were then presented for either 50 ms [100-ms stimulus onset asynchrony (SOA)] or 750 ms (800-ms SOA). The target was presented until the response or until 1,500 ms had elapsed. The target was a filled-in white square (0.70°) located inside one of the boxes and centered 5.5° to the right or left of central fixation. On catch trials (20 %), the target failed to appear and participants were requested to avoid responding.

For all trials, participants were instructed to remain fixated on the center point and to respond to the target as quickly as possible. Participants were instructed to ignore the cues because they were nonpredictive (i.e., half of the targets appeared on the same side as the cue, and half on the opposite side). A short error tone sounded if participants responded too quickly ($RT < 100$ ms), failed to respond within 1,500 ms, or responded on a catch trial.

Procedure Participants performed 100 trials in each of the four body positions (seated, prone-pre, HDNF, and prone-post). All participants completed the four blocks of trials in the same order. First, participants were seated in front of the monitor. Second, they completed the task lying in the prone position on a cushioned table with their head supported upright by a headrest. In the third block, the headrest was removed and participants lowered their heads over the edge of the table, viewing a monitor that was located below the table. Finally, the headrest was replaced, and participants returned their head to the upright position (see Fig. 1). Each block consisted of 50 trials within both the 100- and 800-ms SOA conditions. There were 20 cued, 20 uncued, and 10 catch trials for each of the SOA durations.

Data reduction and analysis The mean reaction times (in milliseconds) from errorless trials were subjected to a 4 (body position: seated, prone-pre, HDNF, prone-post) \times 2 (SOA: 100, 800 ms) \times 2 (trial type: cued, uncued) repeated measures

Fig. 1 Depiction of a participant in the seated position (a), prone with head-up position (b), and in the prone position with the head down and neck flexed (c)



analysis of variance (ANOVA). Errors occurred on less than 1 % of the trials and were not subjected to further analysis. Tukey's HSD procedure (with $\alpha = .05$) was used to further analyze statistically significant main effects and interactions involving more than two means.

Results and discussion

Analyses revealed main effects of body position, $F(3, 42) = 3.53, p < .023$; SOA, $F(1, 14) = 7.45, p < .016$; and trial type, $F(1, 14) = 25.10, p < .001$. The two-way interaction of SOA and trial type was also significant, $F(1, 14) = 90.60, p < .001$. The typical facilitation to cued (376 ms) versus uncued (390 ms) locations was revealed with the short SOA (100 ms), as opposed to inhibition of return to the cued (380 ms) versus uncued (338 ms) locations with the longer SOA (800 ms).

The two-way interaction was superseded by a significant three-way interaction of body position, SOA, and trial type, $F(3, 42) = 6.13, p < .002$. In the HDNF position, the inhibition of return that was observed in the longer SOA condition (800 ms) was significantly attenuated, as compared to when participants were in the other positions (see Table 1 and Fig. 2). In addition, the facilitation was reduced in both the HDNF and prone-post conditions when the SOA was short (100 ms). It is interesting that the reduction in the facilitation effect remained after the participants returned to the prone position, whereas the inhibition-of-return phenomenon reappeared with a magnitude similar to that observed in the seated and prone-pre positions. These results indicated a significant influence of vestibular inputs on the timing of responses to visual stimuli. In addition, the results revealed a change in the time course of the facilitation and inhibition of spatial locations that was dependent on the current and recent body positions.

Experiment 2

The purpose of Experiment 2 was to determine whether the attenuation of cuing effects during HDNF was restricted to reflexive orienting-of-attention tasks. Participants now performed an endogenous cuing task while seated, in a prone position, or in the HDNF position.

Method

Participants A group of 15 undergraduate students and staff from Nipissing University completed this protocol. The participants ranged in age from 20–30 years, and all had corrected-to-normal or normal vision.

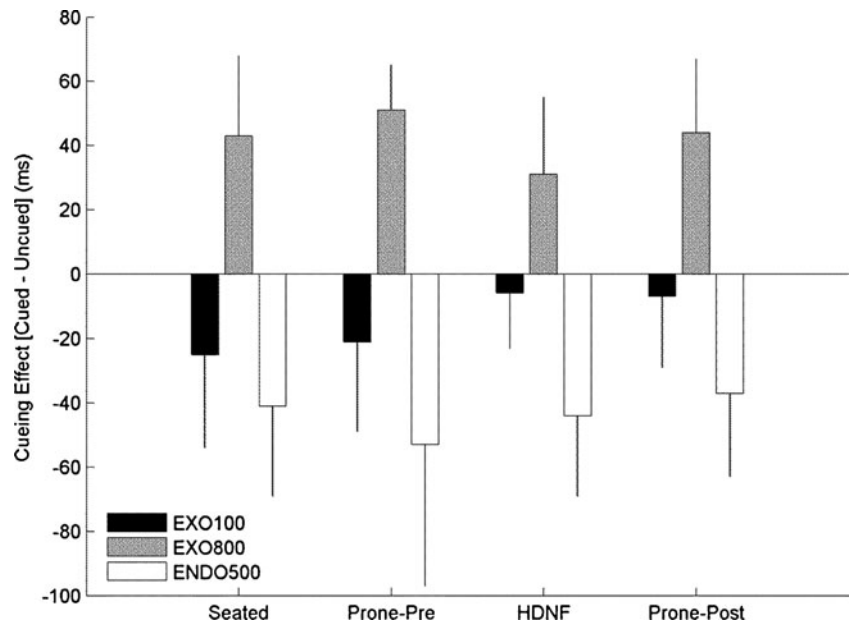
Apparatus and task The equipment used was identical to that of the previous experiment. Participants responded to either target by using the microswitch. Each trial began with a blank black screen (1,000 ms). Following that, a display consisting of the white outlines of two squares (1° per side) located on the horizontal meridian 5° to the left and the right of a central fixation dot (filled white circle: 0.2° diameter) appeared for 1,000 ms. Subsequently, a cue replaced the central fixation dot for 50 ms. The cue was either two arrowheads facing left (\llcorner) or right (\ggcorner), or a neutral cue (\diamond). After the cue, the central fixation dot reappeared for 450 ms. The target then appeared

Table 1 Mean reaction times (in milliseconds, with standard deviations in parentheses) for Experiments 1 (exogenous) and 2 (endogenous), as a function of cuing condition and position (seated, prone-pre, head down with neck flexed [HDNF], and prone-post)

| | Cued | Uncued | Cuing effect | Neutral cue |
|------------------|----------|----------|--------------|-------------|
| Exogenous cuing | | | | |
| SOA 100 | | | | |
| Seated | 382 (43) | 407 (51) | -25 (29) | |
| Prone-pre | 367 (48) | 388 (55) | -21 (28) | |
| HDNF | 383 (59) | 389 (60) | -6 (17) | |
| Prone-post | 370 (53) | 377(54) | -7 (22) | |
| SOA 800 | | | | |
| Seated | 390 (49) | 347 (58) | 43 (25) | |
| Prone-pre | 382 (57) | 331(59) | 51 (14) | |
| HDNF | 382 (57) | 350 (55) | 31 (24) | |
| Prone-post | 367 (51) | 323 (49) | 44 (23) | |
| Endogenous cuing | | | | |
| SOA 500 | | | | |
| Seated | 295 (45) | 336 (55) | -41 (28) | 324 (51) |
| Prone-pre | 288 (43) | 341(66) | -53 (44) | 314 (43) |
| HDNF | 287 (40) | 331(53) | -44 (25) | 309 (42) |
| Prone-post | 279 (40) | 316 (47) | -37 (26) | 255 (55) |

Negative values represent facilitation

Fig. 2 Cuing effects (in milliseconds, with standard deviations), as a function of cuing condition (exogenous 100, exogenous 800, or endogenous 500) and body position (seated, prone-pre, head down with neck flexed [HDNF], or prone-post). Negative values represent facilitation



until the participant responded or until 1,500 ms had elapsed. The target was a filled-in white square (0.70°) located inside one of the boxes. The target failed to appear on catch trials (20 %).

Participants were instructed to fixate the central fixation and to respond by pressing the microswitch. Participants were informed that the directional cues were 80 % predictive. An error was recorded when participants responded too quickly ($RT < 100$), failed to respond within 800 ms, or responded on a catch trial.

Procedure Participants completed two blocks of 60 trials in each of the four body positions (seated, prone-pre, HDNF, and then prone-post). Each block consisted of 32 valid (16 left, 16 right), eight invalid (four right, four left), eight neutral, and 12 catch (four right, four left, four neutral) trials that were presented in a random order. A short break was provided after each block of 60 trials.

Data reduction, analyses, and results

The mean reaction times (ms) from correct trials were subjected to a 4 (body position: seated, prone-pre, HDNF, prone-post) \times 2 (trial type: valid, invalid) repeated measures ANOVA. Errors occurred on less than 2 % of the trials and were not subjected to further analyses. Tukey's HSD was employed to further analyze main effects and significant interactions. The analyses revealed main effects of trial type, $F(1, 14) = 38.85$, $p < .001$, and body position, $F(3, 42) = 5.67$, $p < .003$. The expected facilitation for valid (287 ms) versus invalid (331 ms) locations was observed. In addition, reaction times were shorter in the prone-post (298 ms) than in

the seated (316 ms) or prone-pre (315 ms; HDNF = 309 ms) conditions. However, the two-way interaction failed to reach significance.

General discussion and conclusion

Our results indicate a potential dissociation between reflexive and volitional orienting of visual attention that is dependent on vestibular inputs. Specifically, vestibular stimulation associated with an HDNF body position resulted in an attenuation of visual cuing effects during responses to exogenous cues. In addition, the continued attenuation of the facilitation under a short SOA in the prone-post condition may indicate that some attention processes are dependent on both the current and previous body positions. However, reaction times to previously cued locations were equally long when the targets were cued endogenously, irrespective of body position.

Over the past few decades, differences in human responses to endogenous and exogenous cues have been widely studied (Klein, 2000). The superior colliculus is a neural structure that has been implicated in the moderation of IOR during reflexive and volitional control (Anderson & Rees, 2011; Klein, 2000; Satel, Wang, Trappenberg, & Klein, 2011). Additionally, the superficial and intermediate layers of the superior colliculus (sSC and iSC) have been implicated as significant contributors to multisensory integration (Angelaki et al., 2009; Stein & Stanford, 2008). The sSC is posited to have a primary role during the reflexive response to exogenous cues that leads to the appearance of IOR (Klein, 2000). In comparison, during multisensory integration within the iSC that occurs during responses to endogenous cues, the additional involvement of higher cortical structures such as the frontal eye fields (FEF;

Ro, Farnè, & Chang, 2003) and posterior parietal cortex could lead to the augmentation or dissipation of typical IOR processes (Satel et al., 2011). In the present study, additional multisensory processing within the iSC that was associated with the atypical vestibular input may have led to the observed decrease in IOR during responses to the exogenous cues. In contrast, the continued involvement of the iSC and higher cortical structures during the concurrent integration of top-down (endogenous) input signals and the atypical vestibular input may have allowed for the maintenance of the inhibitory processes.

Overall, the present results reveal integral roles of body position and vestibular input on the control of responses to visual stimuli. Further research on the relationship between vestibular stimulation and visual attention will help us to understand the influences of multisensory integration on movement control.

Author note A Natural Science and Engineering Research Council (NSERC) of Canada grant held by the primary author supported this research. The authors thank two undergraduate students, Graham Scholl and Evan Walsh, for assistance during the collection of the data.

References

- Anderson, E. J., & Rees, G. (2011). Neural correlates of spatial orienting in the human superior colliculus. *Journal of Neurophysiology*, *106*, 2273–2284.
- Angelaki, D. E., Gu, Y., & DeAngelis, G. C. (2009). Multisensory integration: Psychophysics, neurophysiology, and computation. *Current Opinion in Neurobiology*, *19*, 452–458.
- Essandoh, L. K., Duprez, D. A., & Shepherd, J. T. (1998). Reflex constriction of human limb resistance to head-down neck flexion. *Journal of Applied Physiology*, *64*, 767–770.
- Grubb, J. D., Reed, C. L., Bate, S., Garza, J., & Roberts, R. J. (2008). Walking reveals trunk orientation bias for visual attention. *Perception and Psychophysics*, *70*, 688–696. doi:10.3758/PP.70.4.688
- Guerraz, M., Boulin, J., & Vercher, J.-L. (2003). From head orientation to hand control: Evidence of both neck and vestibular involvement in hand drawing. *Experimental Brain Research*, *150*, 40–49.
- Hayes, S. J., Hansen, S., & Elliott, D. (2010). Between person effects on attention and action: Joe and Fred revisited. *Psychological Research*, *74*, 302–312.
- Ishikawa, T., & Miyazawa, T. (1980). Sympathetic responses evoked by vestibular stimulation and their interactions with somatic-sympathetic reflexes. *Journal of the Autonomic Nervous System*, *1*, 243–254.
- Karnath, H. O., Schenkel, P., & Fischer, B. (1991). Trunk orientation as the determining factor of the ‘contralateral’ deficit in the neglect syndrome and as the anchor of the internal representation of body orientation in space. *Brain*, *114*, 1997–2014.
- Kingstone, A., & Pratt, J. (1999). Inhibition of return is composed of attentional and oculomotor processes. *Perception & Psychophysics*, *61*, 1046–1054. doi:10.3758/BF03207612
- Klein, R. M. (2000). Inhibition of return. *Trends in Cognitive Sciences*, *4*, 138–147. doi:10.1016/S1364-6613(00)01452-2
- Paige, G. D., Telford, L., Seidman, S. H., & Barnes, G. R. (1998). Human vestibulo-ocular reflex and its interactions with vision and fixation distance during linear and angular head movement. *Journal of Neurophysiology*, *80*, 2391–2404.
- Posner, M. I., & Cohen, Y. (1984). Components of visual orienting. In H. Bouma & D. G. Bouwhuis (Eds.), *Attention and performance X: Control of language processes* (pp. 531–554). Hillsdale, NJ: Erlbaum.
- Posner, M.I., Nissen, M.J., & Ogden, W.C. (1978). Attended and unattended processing modes: The role of set for spatial location. In J.H.I. Pick & E. Saltzman (Eds.), *Modes of Perceiving and Processing Information* (pp. 137–157). Hillsdale, NJ: Erlbaum.
- Raphan, T., & Cohen, B. (2002). The vestibular-ocular reflex in three dimensions. *Experimental Brain Research*, *145*, 1–27.
- Reed, C. L., Grubb, J. D., & Steele, C. (2006). Hands up: Attentional prioritization of space near the hand. *Journal of Experimental Psychology: Human Perception and Performance*, *32*, 166–177.
- Ro, T., Farnè, A., & Chang, E. (2003). Inhibition of return and the human frontal eye fields. *Experimental Brain Research*, *150*, 290–296.
- Satel, J., Wang, Z., Trappenberg, T. P., & Klein, R. M. (2011). Modeling inhibition of return as short-term depression of early sensory input to the superior colliculus. *Vision Research*, *51*, 987–996.
- Seidman, S. H., Telford, L., & Paige, G. D. (1998). Tilt perception during dynamic linear acceleration. *Experimental Brain Research*, *119*, 307–314.
- Shortt, T. L., & Ray, C. A. (1997). Sympathetic and vascular responses to head-down neck flexion in humans. *American Journal of Physiology*, *272*, H1780–H1784.
- Spence, C., Lloyd, D., McGlone, F., Nicholls, M. E. R., & Driver, J. (2000). Inhibition of return is supramodal: A demonstration between all possible pairings of vision, touch, and audition. *Experimental Brain Research*, *134*, 42–48. doi:10.1007/s002210000442
- Stein, B. E., & Stanford, T. R. (2008). Multisensory integration: Current issues from the perspective of the single neuron. *Nature Reviews Neuroscience*, *9*, 255–266.
- Taylor, T. L., & Klein, R. M. (1998). On the causes and effects of inhibition of return. *Psychonomic Bulletin & Review*, *5*, 625–643. doi:10.3758/BF03208839
- Welsh, T. N., Ray, M., Weeks, D. J., Dewey, D., & Elliott, D. (2009). Does Joe influence Fred’s actions? Not if Fred has autism spectrum disorder. *Brain Research*, *1248*, 141–148.