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The spatial relations between stimulus and response determine an absolute visuo-haptic calibration in pantomime-grasping

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ABSTRACT

Pantomime-grasps entail a response to an area adjacent to (i.e., spatially dissociated pantomime-grasp), or previously occupied by (i.e., no-target pantomime-grasp) a target. Previous work has reported that pantomime-grasps differ kinematically from naturalistic grasps (i.e., grasping a physical target object) – a result taken to evince that pantomime-grasps are perception-based and mediated via relative visual information. However, such actions differ not only in terms of their visual properties, but also because the former precludes haptic feedback related to a target's absolute size. The current study provides four experiments examining whether experimenter-induced haptic feedback influences the information mediating spatially dissociated and no-target pantomime-grasps. Just-noticeable-difference scores were computed to determine whether grasps adhered to, or violated, the *relative* psychophysical properties of Weber's law. Spatially dissociated pantomime-grasps performed with haptic feedback adhered to Weber's law (Experiments 1–3), whereas their no-target pantomime-grasp counterparts violated the law (Experiment 4). Accordingly, we propose that the top-down demands of decoupling stimulus-response relations in spatially dissociated pantomime-grasping renders aperture shaping via a visual percept that is not directly influenced by the integration of haptic feedback. In turn, the decreased top-down demands of no-target pantomime-grasps allows haptic feedback to serve as a reliable sensory resource supporting an absolute visuo-haptic calibration.

1. Introduction

Our ability to recognize and identify a visual object requires that we process the object's *relative* and perceptual properties within an *allocentric* frame of reference (i.e., with respect to other objects). For example, identifying an apple from among different fruits at our local greengrocer is mediated by previous experiences with apples and via allocentric and relative comparisons (e.g., colour, shape, and size) to 'other' fruits. In contrast, if we reach to grasp the apple (i.e., an action task) then maximally effective and efficient motor output requires the computation of the apple's *absolute* properties (e.g., size, shape and location) within an *egocentric* frame of reference (i.e., with respect to our own body). Goodale and Milner's (1992) perception-action model (PAM) asserts that the aforementioned tasks are supported via functionally and anatomically distinct visual processing streams. In particular, the PAM contends that relative and allocentric cues mediate top-down object identification and are supported via visuoperceptual networks residing in the inferotemporal cortex of the ventral visual pathway (James, Culham, Humphrey, Milner, & Goodale, 2003). In turn, the PAM asserts that the absolute and egocentric cues supporting actions are subserved via dedicated visuomotor networks in the posterior parietal cortex of the dorsal visual pathway.

It is, however, important to recognize that some goal-directed actions require motor output that is, in part, specified via an object's relative and allocentric properties. For example, Fig. 1 presents two pantomime-grasping tasks. In the first example (see left panel), a performer is depicted grasping to an area adjacent to a target object (i.e., spatially dissociated pantomime-grasp), whereas in the second example (see right panel) the performer is shown grasping to an area previously occupied by a target object (i.e., no-target pantomime-grasp). In both examples, the performer must regulate their response via top-down (i.e., perception-based) allocentric comparisons between the dissociated stimulus and response (SR) and/or retrieve relative

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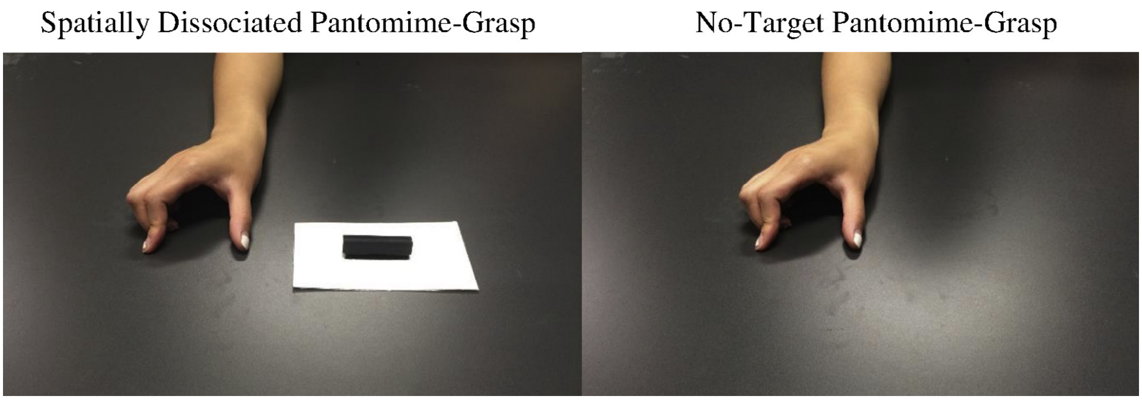

Fig. 1. Exemplar depictions of spatially dissociated and no-target pantomime-grasps. Both conditions entail a common start and movement goal location. For spatially dissociated pantomime-grasps the target object is adjacent to the movement goal location, whereas for no-target pantomime-grasps the participant is required to grasp to the area originally occupied by the target object. In both conditions the target object is unavailable to grasp at the movement goal location.

information about the target from memory. In demonstrating this point, Goodale, Jakobson, and Keillor (1994) had patient DF and healthy controls complete spatially dissociated and no-target pantomime-grasps. DF is an extensively studied individual with a visual form agnosia (i.e., perceptual deficit) arising from bilateral lesions to her lateral occipital cortex (James et al., 2003). In spite of DF's visuoperceptual impairment, she demonstrates preserved naturalistic reaching and grasping – a finding attributed to her intact dorsal visual pathway. Notably, Goodale et al. showed that DF's spatially dissociated and no-target pantomime-grasps did not scale to the veridical size of target objects; more specifically, her performance was no better than her well-documented visuoperceptual deficit. Moreover, evidence from healthy controls has shown that pantomime-grasps produce smaller peak grip apertures (PGAs) than their naturalistic grasping counterparts (Cavina-Pratesi, Kuhn, Ietswaart, & Milner, 2011; Davarpanah Jazi & Heath, 2016; Davarpanah Jazi, Hosang, & Heath, 2015; Davarpanah Jazi, Yau, Westwood, & Heath, 2015; Fukui & Inui, 2013; Westwood, Chapman, & Roy, 2000). Further, work by our group (Holmes, Lohmus, McKinnon, Mulla, & Heath 2013) examined whether pantomime-grasps adhere to, or violate, the *relative* psychophysical principles of Weber's law. The application of Weber's law was based on Ganel, Chajut, & Algom, 2008; Ganel, Chajut, Tanzer, & Algom, 2008 findings showing that perception-based tasks adhere to the law, whereas their naturalistic grasping counterparts violate the law. Holmes et al. showed that pantomime- and naturalistic grasps respectively adhered to and violated Weber's law. Accordingly, Holmes et al. provide rule-based evidence that pantomime-grasps are perception-based and mediated via relative and allocentric visual information. Indeed, the research outlined above adds importantly to the literature insomuch as it provides a framework to understand how the top-down action demands (i.e., dissociating SR spatial relations) of pantomime-grasping influence the nature of the visual information supporting motor output, and also demonstrates the limitations of early neuroimaging studies employing pantomime-grasps as a proxy for naturalistic grasps.

A notable feature of the pantomime-grasps outlined in the previous paragraph is that such actions differed from naturalistic grasping not only in terms of their 'visual' properties, but also because the absence of a physical object in pantomime-grasping precludes the opportunity to integrate terminal haptic feedback. In naturalistic grasping, the performer integrates absolute haptic cues via physically grasping the target object, whereas no such feedback is available in pantomime-grasping. Thus, it is possible that terminal haptic feedback serves as an important sensory cue in determining the nature of the information mediating aperture shaping.[1] In addressing this issue, Schenk (2012) examined DF's pantomime-grasping performance by employing a mirror-box apparatus (see Fig. 1 of that work; see also Bingham, Coats, & Mon-Williams, 2007) allowing for the dissociation between the visual and physical location of a to-be-grasped target object. Schenk reported that DF's pantomime-grasps performed in a block of trials that precluded haptic feedback resulted in motor output that was no better than her visuoperceptual deficit. In turn, DF's pantomime-grasps performed in a block of trials that provided intermittent – but predictable – terminal haptic feedback resulted in metrical aperture scaling. Schenk proposed that DF integrates haptic feedback into her pantomime-grasps to support an absolute 'visuo-haptic' calibration. Although Schenk did not provide a mechanistic account for his findings (cf. Milner, Ganel, & Goodale, 2012; Whitwell & Buckingham, 2013; Whitwell, Milner, Cavina-Pratesi, Byrne, & Goodale, 2014), Whitwell et al. proposed that *if* haptic feedback supports DF's aperture scaling then it may do so via: (1) proprioceptive-based thumb and forefinger feedback serving a feedforward control process that shapes future trial performance and/or (2) an error signal derived from predicted and actual haptic feedback cues that supports an absolute visuo-haptic calibration.

In line with Schenk (2012), recent work by our group (Davarpanah Jazi & Heath, 2016; Davarpanah Jazi, Yau, et al., 2015; Hosang, Chan, Davarpanah Jazi, & Heath, 2016) and others (Bingham et al., 2007) involving neurologically healthy individuals has shown that no-target pantomime-grasps performed with and without terminal haptic feedback are supported via distinct sensory properties (absolute vs. relative). For example, Davarpanah Jazi et al. had participants complete no-target pantomime-grasps without limb and target vision in conditions wherein terminal haptic feedback was unavailable (i.e., PH−) and available (i.e., PH+) at the movement goal location. In particular, the PH− condition represented an exemplar pantomime-grasp involving a response to a location previously occupied by a target object. In contrast, for

[1] Dijkerman and deHaan's (2007) somatosensory processing model (SPM) states that tactile perceptions and actions are mediated via functionally and anatomically dissociable cortical pathways that rely on allocentric and egocentric reference frames, respectively (for review of tactile and haptic frames of reference see Lederman & Klatzky, 2009). According to the SPM, *relative* cues are mediated via a ventral pathway that extends from the anterior parietal cortex (APC) and the secondary somatosensory cortex (SII) to the posterior insula and underlies perceptions. In turn, a dorsal stream extending from the APC and SII to the posterior parietal cortex subserves actions and processes *absolute* tactile cues. Thus, tactile cues for perceptions and actions are mediated via processing characteristics that are comparable to their visual counterparts.