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The Effect of Knowledge of Upcoming Haptic Feedback on Normal and Pantomime Grasps

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Abstract

Normal grasping actions towards real objects are target-directed, mediated via real-time visuomotor control, and provide haptic feedback. Studies of visual form agnosic patient DF suggest that pantomime (pretend) grasps are different; they recruit the visual Ventral stream (inferior temporal cortex), while normal grasps recruit the visual Dorsal stream (posterior parietal cortex). This functional duality underlies the eponymous Two Visual Systems Hypothesis (TVSH). Critics of the TVSH emphasize the multimodal nature of sensory processing and propose a model, termed the Common Source Hypothesis (CSH), of a single more localized system. Existing studies of natural prehension during interleaved trials of normal and pantomime grasps are presented as supporting the CSH, as are reports that pantomime grasps are unsusceptible to knowledge of haptic feedback availability. However, these studies have methodological shortcomings that compromise their results. The current study replicated these experiments while eliminating those methodological shortcomings. Healthy participants performed grasping tasks involving cylinders presented to the participant using a mirror setup, while data on grasp kinematics were recorded. Normal and pantomime grasps were used to recruit the dorsal and ventral streams respectively. We found that when interleaving normal and pantomime grasps and controlling for knowledge of upcoming haptic feedback, pantomime grasps displayed the expected decrements in precision, supporting the TVSH. Additionally, pantomime grasps were susceptible to manipulation of knowledge whereas normal grasps were not, indicating a bifurcation of the visual system by degree of cognitive accessibility. These findings highlight the important role of cognition in mediating grasping actions when a participant knows there will not be haptic feedback on the upcoming grasp.

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The Effect of Knowledge of Upcoming Haptic Feedback on Normal and Pantomime Grasps

Despite remarkable advances in our understanding of the connectional anatomy of various regions of the brain as a result of the technological explosion of the last 30 years, there is still much debate concerning the extent of, and the precise organization of, areas devoted to visual processing and the integration of visual signals for motor planning and fine motor control (Whitwell, Milner, & Goodale, 2014). In recent years, the study of visual perception and action has emerged as a field with a broad cross-disciplinary heritage. Antecedent work in animal lesion studies, clinical case-studies, and on saccadic eye movements informed early forays into the neuroscience of visual cognition and skilled sensorimotor movements like grasping (Goodale, Jakobson, and Keillor, 1994). Much contemporary research in visual cognition is aimed at elucidating the functional connectivity of regions of the visual system, with clinical implications for diseases affecting visual and motor areas of the brain, such as Parkinson's disease. Within this context, the current study attempts to evaluate some recent challenges to a particularly well-accepted model of the visual system's connectivity, in an effort to refine this model and contribute to the increasing precision with which function is being mapped onto anatomical cortical structures in the brain.

The Study of Visual Cognition and Motor Control

Since the turn of the 20th Century, psychologists have explored the role of the brain's visual systems in mediating online visuomotor control (Woodworth, 1899). On the basis of contemporary lesion studies, Schneider (1969) postulated the existence of two anatomically separate visual systems – one for the visual identification of objects (retinotectal pathway), and one for the visual coding of an object's location in space (geniculostriate system). This distinction between systems became known as the 'what' versus the 'where' distinction.

Research over the following decade found support for Schneider’s functional distinction between visual coding for identification and for location, but not for his localization of these activities to retinotectal and geniculostriate areas. Ungerleider and Mishkin (1982) suggested that Schneider’s ‘Two Visual Systems’ were better characterized anatomically as two ‘streams’ of visual information passing along white matter tracts radiating from the striate cortex in the occipital lobe. They identified a ‘ventral stream’ terminating in the inferior temporal cortex and responsible for object identification, and a ‘dorsal stream’ terminating in the posterior parietal cortex and responsible for object location. In the years following, electrophysiological and brain-imaging studies found support for Ungerleider and Mishkin’s proposed anatomical localization of the dorsal and ventral streams (Goodale & Milner, 1992). Ungerleider and Mishkin’s (1982) identification of dorsal and ventral streams with Schneider’s (1969) Two Visual Systems continues to form the theoretical underpinning for current research in visual cognition.

The Two Visual Systems Hypothesis

In 1992, Goodale and Milner authored an expanded account of dorsal and ventral stream functionality by suggesting that these systems not only processed incoming visual information, but also mediated output that makes use of processed visual information, such as motor movements. They suggested that the ventral stream is responsible not only for object identification, but also for general visual perception and object-specific features such as shape, size, colour, and hue; and that the dorsal stream codes both for an object’s location in space, and also mediates actions required to interact with an object, such as grasping. In essence, Goodale and Milner proposed two visuo*motor* systems: a ventral stream mediating visual perception, and a dorsal stream mediating visually-guided action. Compared to Schneider’s ‘what’ versus ‘where’ distinction, Goodale and Milner contended that a ‘what’ versus ‘how’ distinction better reflected the functional dichotomy of the ventral and dorsal streams. Despite their novel emphasis on output motor requirements, Goodale and Milner's hypothesis subsequently became known as the Two Visual Systems Hypothesis (TVSH).

Compelling support for the TVSH first came from Goodale, Milner, Jakobson, and Carey's (1991) report of patient DF, who suffered bilateral lesions to her occipito-temporal cortex (ventral stream) as a result of hypoxia due to carbon monoxide poisoning caused by a malfunctioning water heater (for detail of lesions, see Whitwell et al., 2014). DF suffered profound 'visual-form agnosia', a gross impairment in recognition and discrimination of visually presented objects. Despite these deficits, DF showed preserved visuomotor functioning: she was able to accurately modulate her grasp to match the spatial and geometric properties of objects she reached for, functionality which Goodale and colleagues ascribed to her relatively intact dorsal stream. Goodale *et al*. (1994) tested Patient DF's and healthy controls' performance of 'normal' and 'pantomime' grasps. Normal grasps are 'natural' grasps; they are target-directed and there is an object physically present at the end of the grasp. Pantomime grasps are 'pretend' grasps, such as reaching out beside an object and pretending to pick it up, or being required to briefly remember the position of an object before reaching out to grasp it (i.e. introducing a temporal delay between viewing the object and reaching for the object). In healthy controls, Goodale and colleagues found that while grip aperture was scaled as a function of target size for both normal and pantomime grasps, maximum grip aperture was on average smaller for pantomime grasps than for normal grasps. In addition, other kinematic variables such peak hand velocity and time to peak grip aperture differed between normal and pantomime grasps. Goodale and colleagues found that Patient DF also exhibited intact grip scaling for normal grasps, but she showed no grip scaling during pantomime grasps. DF's dissimilar performance strongly suggested that normal and pantomime grasps were recruiting different neural machinery. Specifically, DF’s preserved grip scaling during normal grasps implied a dorsal-stream mediated process. Moreover, Goodale and colleagues argued that DF’s lack of grip scaling during pantomime grasps reflected her inability to construct perceptual representations of objects, on account of her damaged ventral stream, suggesting that pantomime grasps were being driven by a system that relies on using stored perceptual information (such as the ventral stream; Goodale *et al*., 1994). Later evidence from fMRI studies provided support for this hypothesis that DF’s intact dorsal stream is responsible for her preserved visuomotor control (James, Culham, Humphrey, Milner, & Goodale, 2003).

While initial studies on Patient DF led to the TVSH and established the dorsal stream as responsible for normal grasping, evidence also accumulated for pantomime grasping being mediated by the ventral stream. Studies found that dorsal stream mediated grasping was immune to visual illusions, whereas both perceptual estimations and pantomime grasps were susceptible to such illusions, indicating that pantomime grasping was relying on the same ventral-stream-mediated perceptual mechanisms recruited during the construction of perceptual representations (Haffenden & Goodale, 1998; Westwood, Chapman, & Roy, 2000). Gathering support for this distinction was valuable, as it allowed researchers to test predictions about the TVSH by employing normal and pantomime grasps in experiments to selectively recruit the dorsal and ventral streams respectively.

An Alternative Account for DF’s Performance: The Common Source Hypothesis

Critics of the TVSH propose a system in which there exists a single common pool of visual information and greater interconnectivity between areas associated with visually guided action and perception, emphasizing the multimodal nature of sensory processing (Katz, 2015).

Proponents of this model, termed the Common Source Hypothesis (CSH), explain DF's poor grip scaling during pantomime grasps as resulting from an absence of haptic feedback at the target end-point; that is, during pantomime grasps, no object is physically touched at the end of the grasp. Haptic feedback offers information – such as the width and contours of the object – that can be used to fine-tune grasp aperture over several trials. During normal, but not pantomime grasps, haptic feedback is present and DF may rely on this information to compensate for her perceptual deficits, which could explain her preserved grip scaling during normal, but not pantomime grasps. Bingham, Coates, and Mon-Williams (2007) argued that DF abnormally relies on feedback from one haptic trial to calibrate grasp aperture on the next trial. They proposed that DF fails to show grip scaling during pantomime grasps *not* because she is unable to form a perceptual representation of the object as the TVSH suggests, but rather because she has no opportunity to learn to modulate her grasp over a series of trials. In short, they suggested that haptic feedback is critical to maintaining the 'natural prehension' observed during normal grasps when an object is present. Bingham *et al*. defined 'prehension' according to Jeannerod's (1988) definition: a target-directed grasping movement of the hand with a 'transport component' involving translational motion of the hand, and a 'grasp component' involving the in-flight pre-shaping of the fingers in preparation for closing around the object. Bingham *et al*. (2007) hypothesized that if haptic feedback could somehow be provided during pantomime grasps, such haptic-rich 'pantomime' grasps would be indistinguishable from normal grasps in healthy controls, and for such grasps DF would exhibit preserved grip-scaling.

An Experimental Challenge to the TVSH: Bingham *et al*. (2007)

To test their hypotheses, Bingham *et al*. (2007) used a mirror-apparatus which allowed the experimenter to manipulate haptic feedback (see Appendix A). Their apparatus merits a brief explanation here, as it provides a representative example of an experimental set-up commonly used in grasping studies. Participants were seated at a table facing the mirror-apparatus, and objects could be placed both in front of the mirror and behind the mirror. Objects placed in front of the mirror were reflected in the mirror, producing a virtual image of the reflected object at the mirror-symmetrical position behind the mirror. Objects placed behind the mirror at this mirror-symmetrical position were spatially coincident with the position at which the virtual image appeared (reflected from the object in front of the mirror), so the participant could feel an object at the end of the grasp. Participants always reached towards the virtual image behind the mirror. Placing an object in front of the mirror and placing an identical object behind the mirror provided haptic feedback to the grasp. Placing an object only in front of the mirror permitted grasps to be directed at a visually-presented object while denying haptic feedback; that is, an object could be seen at the location behind the mirror but could not be grasped at that location. In this way, the experimenter could control whether haptic feedback was provided at the end of the grasp. Thus, when a participant knew whether they would receive haptic feedback at the end of their grasp on the upcoming trial, haptic trials (object present) represented an experimental analogue for normal grasps, while non-haptic trials (object absent) constituted pantomime grasps. While there were some decrements in grasp precision for normal grasps using this apparatus due to procedural constraints not mentioned here, these effects are not relevant to the current discussion (see Whitwell, Lambert, and Goodale [2008] for a discussion of the differences between closed and open loop testing).

Bingham *et al*. (2007) compared grasp kinematics from consecutive non-haptic trials (pantomime condition) to grasp kinematics when haptic and non-haptic trials were randomly interleaved (random condition). They reported natural prehension on the non-haptic trials in the random condition – that is, they observed no differences between the haptic (ostensibly normal) and the non-haptic (ostensibly pantomime) grasps within the random condition itself – whereas grasps in the purely pantomime condition still showed the normal decrements associated with pantomime grasping. They suggested that the intermittent haptic feedback in the random condition provided an opportunity for the visual system to learn between grasps; to use the information provided on the haptic trials to ‘calibrate’ grip scaling during the non-haptic trials. Since participants produced natural prehension akin to normal dorsal-stream mediated grasps on non-haptic trials when intermittent haptic feedback was provided, Bingham and colleagues concluded that the dorsal stream is able to support pantomime grasping by relying on haptic feedback over a series of trials, challenging the TVSH’s contention that the dorsal stream mediates only normal, and not pantomime grasps.

Theoretical Rebuttal of Bingham *et al*. (2007)

An anonymous reviewer pointed out that in Bingham *et al*.’s (2007) pantomime condition, participants were aware of the fact that they would be given a number of consecutive non-haptic trials; thus, trials in the pantomime condition were accompanied by the knowledge that the object would not be present on each upcoming trial. Conversely, in the random condition, participants had no knowledge of whether the upcoming visually presented object would be physically present or absent on the upcoming trial. Thus, the knowledge of upcoming haptic feedback was confounded with the condition. In short, Bingham *et al*. neglected to control for knowledge.

The anonymous reviewer even proffered an explanation for Bingham *et al*.’s results, suggesting that the absence of knowledge in the random condition may have caused the visual system to adopt a cognitive strategy of consistently recruiting the dorsal stream, even for non-haptic (supposedly pantomime) grasps, which would explain the dorsal-like natural prehension observed. This explanation may be clarified by the following example: Let us stipulate that reaching to an object known to be present (haptic trials) recruits the dorsal stream, and that reaching to an object known to be absent (non-haptic trials) recruits the ventral stream. The question now arises, what happens on trials when it it *not known* whether an object will be present, as in Bingham *et al*.'s random condition? One possible answer is that such trials would recruit the system specialized for visually-guided action, the dorsal stream. In that case, we would expect the random condition pantomime (non-haptic) grasp responses to be more like dorsal stream responses than like ventral stream responses. That is what Bingham *et al*. found. Thus, we have two accounts of Bingham *et al*.'s result available: the CSH; and a version of the TVSH in which, under the peculiar conditions of Bingham *et al*.'s laboratory experiment, non-haptic (ostensibly pantomime) grasps were in fact mediated by the fully functioning dorsal stream.

Under the anonymous reviewer's account, the natural prehension observed by Bingham *et al*. in their random condition could be explained by a cognitive switch to recruiting the dorsal stream when faced with uncertainty about the availability of upcoming haptic feedback. But is this explanation plausible? There is some theoretical rationale to think so. As mentioned previously, dorsal stream grasps are unaffected by visual illusions, while ventral stream grasps are susceptible to visual illusions (Westwood *et al*., 2000). In addition, the dorsal stream appears to be unable to use information about the availability of upcoming visual feedback to modulate future grasps (Whitwell *et al*., 2008). These phenomena indicate that the degree of cognitive supervision afforded to actions mediated by the dorsal and ventral streams differs between the two streams. Dorsal stream immunity to visual illusions suggests that the dorsal stream is a largely unconscious pathway to which there is little cognitive access, while ventral stream susceptibility to visual illusions suggests that the ventral stream is characterized by some degree of cognitive access, implicating more conscious, cognitively-penetrable mechanisms.

Unconscious processes are usually fast, highly efficient due to their capacity for parallel processing, and require relatively little cognitive effort; in contrast, conscious processes are usually slower, occur serially, and require greater cognitive effort (Breedlove & Watson, 2013). Since the brain has limited capacity to consciously mediate tasks, control centers in the brain will attempt to minimize cognitive load by preferentially relegating tasks to unconscious cognitive systems unless there is compelling reason to do otherwise. Thus, if some task-1 reasonably approximates another task-2 for which the brain already has a specialized unconscious system, the brain will recruit the task-2-specialized unconscious system to perform task-1, rather than spend greater cognitive effort by employing conscious oversight to perform task-1.

From this perspective, we would predict that the unconscious dorsal stream would be recruited for tasks that reasonably approximate normal grasping tasks. In other words, Bingham *et al*.’s task involving grasping to an object when it is *not known* whether the object will be present (random condition) may be similar enough to normal grasping to simply recruit the dorsal stream. Put another way, Bingham *et al*.’s random condition may *not* be *dissimilar* enough from normal grasping to provoke a shift toward recruiting the ventral stream, in the way that Bingham *et al*.’s task involving grasping to objects that are *known not to be present* (pantomime grasping, with knowledge) clearly does elicit ventral stream oversight.

In their response to the anonymous reviewer, Bingham *et al*. (2007) offered their opinion that the “alterations in behavior are driven by the presence of [haptic] feedback rather than a shift in cognitive strategy” (p. 294), although they did not provide empirical evidence to substantiate their claim. Nonetheless, despite theoretical rationale supporting the idea of dorsal stream intervention in the absence of knowledge of upcoming haptic feedback, the empirical question regarding the mechanism behind Bingham *et al*.'s phenomenon remained unanswered. Was the natural prehension Bingham *et al*. observed during interleaved haptic and non-haptic trials being driven by: the absence of knowledge, or the intermittent haptic feedback?

Testing the Alternatives: Schenk's (2012) Claim of Having Manipulated Knowledge

In an effort to distinguish between the two aforementioned possibilities, Schenk (2012) claimed to have manipulated knowledge of upcoming object presence or absence during randomized haptic and non-haptic trials with patient DF and with healthy controls. For this manipulation, Schenk used a red Light-Emitting Diode (LED) to cue the participant to the presence or absence of the object for each upcoming trial. Schenk found that healthy controls did not differ in their grip-scaling between what he called his knowledge and no-knowledge conditions. Furthermore, Schenk found that DF's performance was within the normal range of grasping behavior. Schenk thus concluded that haptic feedback, rather than knowledge, was responsible for DF's performance, a finding that would support the CSH.

It is apparent, however, that in spite of Schenk's claim to the contrary, he did not in fact manipulate knowledge. To manipulate knowledge, one needs both a condition in which the participant *has* knowledge of what kind of trial they are about to receive, and a condition in which the participant *does not* have such knowledge. Schenk had only the former type of condition. Although Schenk drew his conclusions on the assumption that he had manipulated knowledge of upcoming haptic feedback (what he called the "expectation of encountering a physical object"), even his own report indicates that he did not manipulate knowledge. He states that "grasping performance is the same for trials where she [DF] expected an object and for those where no object was expected" (Schenk, 2012, p. 2016). However, this sentence may be rephrased as follows while still retaining its meaning: grasping performance is the same for trials where DF *expected an object* and for those where she *expected no object*. Critically, in both of Schenk's conditions, the participant *had expectation*; that is, they had knowledge of whether an object was going to be present or absent on each upcoming trial, which was indicated by the state of the red LED.

There have been other criticisms of Schenk's (2012) study, including a theory-based argument by Milner, Ganel, and Goodale (2012) which asks the inevitable question of Schenk's data: if DF truly does rely on past haptic information as opposed to current visual information to modulate grasps, then her performance on trial n+1 should vary only as a function of the size of the object that she grasped on trial n. Schenk's data, however, do not support this prediction. In an empirical response to Schenk's (2012) experiment, Whitwell, Milner, Cavina-Pratesi, Barat, and Goodale (2015) compared DF's grip scaling during visually and haptically congruent trials (an ecologically 'normal' grasping condition) to trials in which haptic feedback remained at an intermediate constant width, while visual presentation varied. DF's grip scaling reflected the visually presented target objects rather than the consistent haptic width, challenging the position that DF relies on haptic feedback to accurately modulate her grasps to target size. However, for the purposes of the current study we will address the fact that Schenk did not manipulate knowledge of upcoming haptic feedback in his 2012 study, which casts doubt on his claim that haptic feedback, rather than knowledge, is responsible for the grasping performance of patient DF and of healthy controls.

Purpose of the Current Study, Independent Variables, and Dependent Variables

The goals of the current study are two-fold: Firstly, to determine whether the natural prehension Bingham *et al*. (2007) observed during randomly interleaved haptic and non-haptic trials is driven by the absence of knowledge of upcoming haptic feedback, or by the intermittent haptic feedback provided; Secondly, to determine whether normal and pantomime grasps differ in the extent to which they are susceptible to knowledge of upcoming haptic feedback. To pursue these goals, the current study will entail partial replications of the experiments performed by Bingham *et al*., and Schenk (2012). However, the current study will differ in that our replication of Bingham *et al*.'s experiment will *control* for knowledge (to achieve the first goal), and our replication of Schenk's experiment will actually *manipulate* knowledge (to achieve the second goal).

Participants will reach towards and grasp small wooden objects while data on hand configuration and position are recorded, using specialized cameras and infra-red markers placed on the hand and wrist. The experimental setup employed by Bingham *et al*. will be used (see Appendix A). Grasping will be performed 'open loop', meaning that vision will be occluded from movement onset. Participants will wear goggles that allow the experimenter to enable or occlude participants' vision. At the start of each trial the goggles will become transparent, and the participant will view the object visually presented, before reaching out to grasp the object. At movement onset, the goggles become instantly opaque, and kinematic data recording begins.

There are five independent variables, three of which vary within-condition (object size, reach distance, and haptic feedback) and two of which vary between conditions (knowledge of upcoming haptic feedback, and presentation). Object size will be manipulated by using three cylinders of differing widths but equal heights, as target objects. Reach distance will be manipulated by having the target object presented at one of two positions (see Appendix A). Haptic feedback will be manipulated as follows: Both on trials involving haptic feedback (haptic trials), and on trials with no haptic feedback (non-haptic trials), an object will be visually presented in front of the mirror; on haptic trials, an identical cylinder to the one visually presented will be placed at the mirror-symmetrical position behind the mirror; on non-haptic trials, *no* object will be placed at the mirror-symmetrical position behind the mirror. Knowledge of upcoming haptic feedback will be manipulated by either explicitly informing the participant of each upcoming trial type (haptic vs. non-haptic), or not informing the participant of the upcoming trial type. Presentation will be manipulated by administering haptic or non-haptic trials consecutively, or by presenting intermixed haptic and non-haptic trials.

The experiment will involve five conditions which differ in terms of haptic feedback and knowledge of upcoming haptic feedback: 1. Block Haptic (BH), comprising 18 consecutive haptic trials; 2. Block Non-Haptic (BNH), comprising 18 consecutive non-haptic trials; 3. Alternating (ALT), comprising 36 trials uniformly alternating between haptic and non-haptic, during which the participant will be informed of the upcoming trial type before each trial; 4. Random with Knowledge (RK), comprising 36 trials pseudo-randomly alternating between haptic and non-haptic, 18 trials of each type, during which the participant will be informed of the upcoming trial type before each trial; and 5. Random No Knowledge (RNK), in which the participant will be presented with the same 36 trials as in the RK condition, but will not be informed of each upcoming trial type. Thus, data collection for a single participant will acquire 144 trials in total. In addition, the nature of each condition will be explained to the participant before commencing testing.

In terms of knowledge, the participant will have knowledge of upcoming haptic feedback for every trial in conditions 1, 2, 3, and 4: either by knowing that in the current condition, all trials will be haptic (BH condition) or non-haptic (BNH condition), providing *implicit* knowledge of upcoming haptic feedback for every trial; or by being *explicitly* informed of each upcoming trial type, haptic or non-haptic, before each individual trial (ALT and RK conditions). Only in condition 5, the RNK condition, will participants *not* have knowledge of upcoming haptic feedback for each trial.

In terms of haptic feedback, participants will receive continuous haptic feedback in condition 1 (BH), and a continuous *absence of* haptic feedback in condition 2 (BNH). The BH and BNH conditions together constitute the 'Blocked' presentation conditions. Participants will receive intermittent haptic feedback in conditions 3, 4, and 5 (ALT, RK, and RNK). The ALT, RK, and RNK conditions together constitute the 'Not-Blocked' presentation conditions.

Five dependent variables will be calculated from the kinematic data: reaction time, peak hand velocity, peak grip aperture, final grip aperture, and slopes. Reaction time is defined as the time from the start of the trial (when the object becomes visible) to movement onset. Peak hand velocity is the maximum in-flight speed of the hand during the reach, assessed from a single point on the hand. Peak grip aperture is the maximum distance between index finger and thumb that occurs during the reach when the hand opens to grasp the object. Final grip aperture is the average distance between index finger and thumb during the end of a non-haptic grasp when that aperture is maintained in a rigid 'c-shape'; the time over which the average is calculated is determined by pre-set thresholds for hand movement. Slopes provide a measure of grip-scaling, and refer to peak grip aperture as a function of target size, which is calculated from the peak in-flight grip aperture and the diameter (i.e. the width) of the cylinder visually presented on a given trial.

Predictions and Hypotheses

The major predictions made in this study are best illustrated by referring to the comparisons made by Bingham *et al*. (2007) and Schenk (2012). Bingham *et al*. compared condition 2 (BNH – with *implicit* knowledge of upcoming haptic feedback) to condition 4 (RNK – no knowledge of upcoming haptic feedback). The current study will compare condition 2 (BNH) to condition 3 (RK – with *explicit* knowledge of upcoming haptic feedback), thus controlling for knowledge by ensuring that in both conditions, participants have knowledge (either implicit or explicit) of upcoming haptic feedback. For our first prediction, we expect that non-haptic and haptic trials in the RK condition will *not* be similar to each-other, that is, the non-haptic trials will *not* show natural prehension – rather, they will look like pantomime grasps. Based on prior work by Goodale *et al*. (1994) regarding pantomime grasps, we predict that non-haptic trials in the RK condition will elicit similar grip scaling and peak grip aperture as non-haptic trials in the BNH condition. This prediction follows from the fact that once participants have knowledge of upcoming haptic feedback as in the RK condition, if we assume that the intermittent haptic feedback does not support pantomime grasping, then haptic and non-haptic grasps become just like normal and pantomime grasps respectively, which are already known to differ on a number of kinematic variables (Goodale *et al*., 1994).

Schenk compared condition 3, the RK condition, to another condition which, in all relevant respects, was also an RK condition. In short, Schenk compared condition 3 to itself. The current study will compare condition 3 (RK) to condition 4 (RNK), thus manipulating knowledge of upcoming haptic feedback. For our second prediction, again informed by Goodale *et al*. (1994), we expect to find that haptic trials in the RK and RNK conditions will elicit similar grip scaling, peak grip aperture, and peak hand velocity; non-haptic trials we expect will differ between the RK and RNK conditions on these three dependent variables. This prediction emerges from: the assumption that our first prediction is borne out and haptic trials are found to differ from non-haptic trials in the RK condition and; the understanding that haptic trials evoke normal grasping which engages the dorsal stream, which appears to be cognitively impenetrable, and therefore dorsal-mediated normal grasps should be unaffected by declarative information such as knowledge of upcoming haptic feedback. Conversely, non-haptic trials evoke pantomime grasping which engages the ventral stream (at least when there is knowledge that the upcoming grasp is non-haptic, as in the non-haptic trials of the RK condition), which appears to be cognitively accessible, and thus ventral-mediated pantomime grasps will likely be influenced by knowledge of upcoming haptic feedback. As mentioned previously, empirical work has found that dorsal stream grasps are unaffected by explicit knowledge of upcoming *visual* feedback (Whitwell *et al*., 2008). It seems likely, therefore, that dorsal stream grasps are also immune to explicit knowledge of upcoming *haptic* feedback.

For our final prediction, we expect to observe the normal decrements in performance for pantomime grasps (BNH condition) compared to normal grasps (BH condition), as reported by others previously (Bingham *et al*., 2007; Goodale *et al*., 1994; Westwood *et al*., 2000). Specifically, based on recent work by Whitwell, Ganel, Byrne, and Goodale (2015) whose results include the five dependent variables used in the current study, we expect that the BNH and BH conditions will differ on all five dependent variables, and moreover, that the difference in grip scaling (slopes values) will be greater between the BNH and BH conditions than for any other pair-wise comparison of grip scaling for haptic and non-haptic trials involving any combination of conditions.

In summary, we may distill our predictions down into three hypotheses which capture the nature of the visuomotor system from the perspective of the TVSH: (1) When controlling for knowledge, interleaving haptic and non-haptic trials will *not* result in natural prehension on the non-haptic trials, rather, such trials will show pantomime-like prehension; (2) non-haptic (pantomime) grasps will be susceptible to knowledge; and (3) pantomime grasps will show decrements in precision and differences in several kinematic variables compared to normal grasps.

Method

Overview

Participants were recruited to take part in a study on visual cognition which involved reaching for and grasping small wooden objects while data on hand configuration and position were recorded. Specialized cameras, along with infra-red LEDs attached to the hand, were used to collect positional data. Following data collection, preliminary analyses were performed offline using in-house software. All procedures were approved by the local ethics committee and conducted in accordance with ethics regulations.

Participants

Thirty-seven right-handed participants with normal or corrected-to-normal vision were recruited at the University of Western Ontario. All participants were undergraduate students. Seven participants were excluded from analyses for not completing the experimental portion of the study. The remaining 30 participants comprised 20 females and 10 males, aged 18 to 57 years (M = 22.4, SD = 7.99). Participants provided written and informed consent prior to participating in the study. Participants were compensated $10 for their time, and had no previous experience with the experiment or with similar experiments.

Apparatus and Experimental Setup

The experimental setup employed a mirror-apparatus that allowed the experimenter to manipulate haptic feedback (see Appendix A for details of the experimental setup). The mirror-apparatus included a mirror with the reflective side positioned at a 45-degree angle to the edge of the table nearest the participant. When facing the mirror-apparatus, the participant performed their reach in the sagittal plane, perpendicular to the edge of the table.

Objects could be placed both in front of the mirror and behind the mirror. Objects placed in front of the mirror were situated between the participant and the reflective surface of the mirror; these objects were reflected in the mirror, producing a virtual image of the reflected object that appeared at the mirror-symmetrical position behind the mirror. Objects placed behind the mirror at this mirror-symmetrical position were spatially coincident with the position at which the virtual image appeared (reflected from the object in front of the mirror), so the participant could feel an object at the end of the reach.

A rigid foam board fixed to the edge of the table closest to the participant, in front of the mirror, occluded direct observation of the object placed in front of the mirror. Consequently, when a participant was correctly positioned and facing the mirror-apparatus, the object placed in front of the mirror could only be seen reflected in the mirror.

Objects could be placed at one of two positions in front of the mirror, and at one of two corresponding mirror-symmetrical positions behind the mirror. Thus, grasps could be made towards an object placed either 10cm from the grasp start-point (near reach), or 20cm from the grasp start-point (far reach). Four thin wooden platforms, each 10cm square, were fixed to the table and marked the four positions at which objects could be placed (see Appendix A).

Participants always performed their reach behind the mirror, aimed towards the position at which the virtual image appeared. Placing an object in front of the mirror and placing an identical object behind the mirror provided haptic feedback to that grasp – these grasps constituted ‘haptic trials’. Placing an object only in front of the mirror permitted grasps to be directed at a visually-presented object while denying haptic feedback; that is, an object could be seen at the location behind the mirror but could not be grasped at that location – these grasps constituted ‘non-haptic trials’.

When the participant knew whether the upcoming grasp was going to be a haptic trial or a non-haptic trial (that is, they had *knowledge* of upcoming haptic feedback), then haptic and non-haptic trials represented normal and pantomime grasps respectively.

Target objects placed in front of the mirror (those visually presented to the participant) were three wooden cylinders of uniform height (70mm) and of three different widths: small (35mm); medium (48mm); and large (60mm). Each of the three target objects placed in front of the mirror had an identical counterpart that was placed behind the mirror during haptic trials. Thus, six objects were used in total; three pairs of identical objects. Objects were painted matte black, and each object had a shallow hole at the axis on one face of the cylinder. The hole on the face of each object accommodated a centrally situated raised pin on each of the four placement platforms, which ensured that each object was placed in the same position on the platform on any given trial.

The entire mirror-apparatus was positioned on a table, facing the participant (see Appendix A). A button, situated on a low-raised wooden platform painted matte black, was placed 10cm away from the edge of the table closest to the participant, and 14cm to the right of and 10cm in front of the closest object position. The button was the start position for the participants’ hand at the beginning of each trial, and registered movement onset when released.

Three infrared emitting diodes (IREDs) were attached with medical tape to the participant’s right hand: one at the thumb nail, one at the index finger nail, and one at the proximal end of the index finger on the dorsal face. The medical tape used to secure the IREDs was cut into very thin strips prior to application, approximately 5mm wide, so as to minimally cover the surfaces of the finger tips which provide grip when grasping an object. The IREDs were positioned such that when the participant's thumb and index finger formed a pincer grasp, the IREDs faced upwards towards the ceiling. The three wires extending from the three IREDs were secured to the participant's wrist at the dorsal face by an additional piece of tape, to ensure that any tugging on the wires leading away from the hand did not displace the IREDs. Attachment of the IREDs did not impede regular movement of the hand or the participant's ability to grasp objects.

Positional data for the IREDs was recorded with a sampling frequency of 200Hz by an OPTOTRACK™ 3020 (Northern Digital, Waterloo, ON, Canada). The Optotrack system comprised three cameras which tracked the position of each IRED in 3D space, with a 3D accuracy of 0.1mm. The three cameras were mounted linearly in a plastic frame approximately 1m wide, with one camera at either end and one camera situated centrally. The frame was mounted horizontally on the ceiling approximately 2m above and 2m away from the surface of the table on which the mirror-apparatus was placed.

Visual feedback was manipulated using goggles, worn by all participants during the experiment, with Liquid Crystal Display (LCD) lenses that could switch between transparent and opaque states (PLATO goggles; Translucent Technologies, Toronto, ON, Canada). The goggles' default state was opaque, which prevented participants from observing the experimenter's actions between trials, and also prevented them from observing their own actions after movement onset. The switch between transparent and opaque states occurred in less than 2ms (that is, two one-thousandths of a second), which for the purposes of experiments in visual cognition is instantaneous. The goggles allowed for visual 'open loop' testing, a common experimental paradigm in studies of manual grasping in which vision is occluded after movement onset; that is, participants could not see the target object or their own hand in motion after beginning to move their hand. The goggles' frame allowed them to be worn over glasses, or under a religious head-covering such as a turban or hijab, but participants were asked to remove baseball caps if they were wearing them.

Experimental Design

Each participant was tested across five conditions which differed in terms of the availability of haptic feedback, and knowledge of the availability of upcoming haptic feedback. The five conditions were: 1. Block Haptic (BH), comprising 18 consecutive haptic trials. On BH trials, we hold that participants have knowledge about the availability of haptic feedback as they begin a trial. 2. Block Non-Haptic (BNH), comprising 18 consecutive non-haptic trials. On BNH trials, we hold that participants have knowledge about the unavailability of haptic feedback as they begin a trial. 3. Alternating (ALT), comprising 36 trials uniformly alternating between haptic and non-haptic, during which the participant was informed of the upcoming trial type before each trial. On ALT trials, participants are given knowledge about the availability of haptic feedback before they begin a trial. 4. Random with Knowledge (RK), comprising 36 trials pseudo-randomly alternating between haptic and non-haptic, 18 trials of each type, during which the participant was informed of the upcoming trial type before each trial. On RK trials, participants are given knowledge about the availability of haptic feedback before they begin a trial. 5. Random No Knowledge (RNK), in which the participant was presented with the same order of 36 trials as in the RK condition, but was not informed of each upcoming trial type. Thus, on RNK trials, the participant has no knowledge of the upcoming trial type as they begin the trial. Data collection for a single participant required 144 trials in total. The presentation order of the 5 conditions was counterbalanced across participants.

In the BH and BNH conditions, each block comprised 18 trials in which six possible combinations of two target positions (near, far) and three object sizes (small, medium, large) were presented three times each in a pseudo-random order. The ALT, RK, and RNK conditions each consisted of 36 trials in which the six combinations of target position and object size were presented six times each, in a pseudo-random order; three on haptic trials and three on non-haptic trials. For the ALT condition, half the participants began with a haptic trial, and half began with a non-haptic trial. In addition, within each participant, the order of trials with respect to object size and target position was identical between the BH and BNH conditions, and between the RK and RNK conditions.

For each participant, pseudo-random ordering of all 144 trials was performed using Microsoft Excel to create a list of trials, grouped by condition, and then assigning each trial a number between 0 and 1 using the program's random number generator, and sorting the trials by their associated random number from highest to lowest, within each condition. Due to the large number of independent variables, and the natural limitations on the total number of trials due to fatigue effects, each permutation of independent variables (each 'unique' trial) was only repeated three times. Accordingly, certain constraints were imposed on the pseudo-random ordering of trials for each participant, in an attempt to guard against detrimental carry-over effects that were predicted to result from sequences of similar trials grouped closely together. As a consequence, ordering of trials was only pseudo-random, and not truly random, due to the following constraints: across all conditions, no object size or target position was presented serially more than twice; and in the RK and RNK conditions, no more than 3 haptic or 3 non-haptic trials were presented consecutively.

Dependent Measures

Grasping behavior was operationally defined *a priori* in terms of five characteristics of manual motor movements: reaction time, peak hand velocity, peak grip aperture, final grip aperture, and slopes. Reaction time was defined as the time from the start of the trial (when the object became visible to the participant) to movement onset (when the participant's hand lifted off the start button). Peak hand velocity was the maximum in-flight speed of the hand during the reach, measured by the IRED at the proximal end of the index finger. Peak grip aperture was the maximum in-flight distance between the IRED at the distal end of the index finger and the IRED on the thumb. Final grip aperture was the average distance between the IRED at the distal end of the index finger and the IRED on the thumb during the end of a non-haptic grasp when that aperture was maintained in a rigid 'c-shape'. Slopes refer to peak grip aperture as a function of target size, which was calculated from the peak in-flight grip aperture and the diameter (i.e. the width) of the cylinder visually presented on a given trial.

Procedure

Prior to data collection. Participants were recruited through posters placed around campus (see Appendix B). The participant and researcher corresponded by email to arrange a testing time. The researcher met participants in the waiting area on the second floor of the Brain and Mind Institute (BMI) at Western University, and admitted them to the testing area. Participants read the Letter of Information (see Appendix C) and signed the Informed Consent Form (see Appendix D). Before signing the Informed Consent Form, participants were questioned to ensure they understood what their participation would require, and were told that after signing they could leave at any time without penalty and would still receive credit for participation.

After signing the Informed Consent Form, participants were seated at a table facing the mirror-apparatus, such that their midline bisected the gap made by the edge of the occluding board and the nearest edge of the mirror (see Appendix A). The participant was asked to remove any bulky items of clothing, such as their coat, which might interfere with their freedom of grasping. Participants were also advised to wear any clothing other than their coat that they had with them (such as a sweater) to make themselves comfortable with the ambient temperature, as after beginning the experiment the participant would not be able to put on or remove extra layers of clothing. The experimenter turned on the Optotrack and the computer connected to the Optotrack, which ran the program for data collection. While the computer booted up, the experimenter explained the task to the participant and attached the IREDs to the participant's right hand in the manner detailed in the Apparatus section. After the computer booted up and the IREDs were attached, the experimenter checked the feedback from each IRED to ensure that they were all functioning and that all grasping motions were within the range of the Optotrack cameras.

After the IREDs were checked, the participant was introduced to the six target objects and was taught the correct grasping motion for haptic and for non-haptic grasps. Specifically, for haptic grasps the participant was instructed to approach the grasp from the side of the object, to grasp with thumb and index finger only (pincer grip), and to grasp near the top of the object, so that the object itself did not occlude the IRED attached to the thumbnail with respect to the Optotrack. After grasping the object, participants were instructed that they were to move the object vertically upwards, laterally to the right, and then place the object on the table.

For non-haptic grasps, the participant was instructed to perform a pantomime or 'pretend' grasp, using thumb and index finger, such that their final grip aperture (their 'grasp') was a manual estimation of the size of the visually presented object. The participant was explicitly instructed to ensure that their in-flight grip aperture was wider than their final grip aperture; that is, to ensure they actually opened and closed their hand as if they were grasping the imaginary object. Participants were instructed that after ‘grasping’ the imaginary object, they were to pantomime the same procedure as for haptic grasps; that is, to pantomime moving the imaginary object vertically upwards, laterally to the right, and then pantomime placing the imaginary object on the table. Participants were also asked to maintain a steady grip aperture on the imaginary object while moving their hand, to obtain a stable grip aperture measurement.

Participants were instructed to perform all grasps at a natural speed, neither taking time to study the position of the object seen in the mirror, nor racing towards to the object to pick it up. Participants were instructed to keep their thumb and index finger pressed together at all times other than during target-directed forward grasps; that is, thumb and index finger were pressed together while depressing the start button between trials, and also during the return movement of the hand from the outstretched position after finishing a grasp. All verbal instructions were accompanied by demonstrations from the experimenter.

After learning the correct grasping procedure, participants were introduced to the mirror-apparatus and the LCD goggles, and were informed about the nature of each of the five conditions in the experiment. The goggles were then placed on the participant’s head and positioned comfortably. At this point, the experimenter checked that all pieces of equipment – the goggles, the Optotrack, the IREDs, and the data-collection program – were turned on and functioning properly, and that the participant and mirror-apparatus were suitably positioned. Participants then performed 15 practice trials during which no data were recorded: five haptic trials modeling the BH condition; five non-haptic trials modeling the BNH condition; and five pseudo-randomized trials modeling the RNK condition. If the participant made errors in grasping behavior during the practice trials, the experimenter informed the participant and gave them further instruction in the correct grasping technique.

Data collection. Data collection began after completion of the 15 practice trials. The experimenter used a printed-out checklist of all 144 trials to determine the order of the conditions and the placement of the objects on each trial (see Appendix E for a sample checklist). If the experimenter noticed that they themselves had made an error in trial administration, such as presenting the wrong pair of objects, the experimenter made a note of the error on the checklist next to the faulty trial but did not re-administer the trial. If the participant made an error in grasping or in some way responded unexpectedly, for example by failing to initiate a grasp, fumbling the target object, or failing to contact the object on a haptic trial, the experimenter provided verbal guidance to the participant on grasping technique, if appropriate, but the experimenter did not halt the experiment or re-administer the trial. A trial was only re-administered when the apparatus failed to work *and* the participant had not been presented with any information about the upcoming trial; for example, in situations where the goggles did not become transparent at the start of a trial. The experimenter kept hand-written notes on the checklist of any deviations from the expected procedure during testing.

Before the start of each trial, while the participant’s goggles were opaque, the experimenter placed an object in front of the mirror. If the trial was a haptic trial, an identical object was placed at the mirror-symmetrical position behind the mirror; if the trial was non-haptic, no object was placed behind the mirror. On haptic trials, the size (small, medium, large) and position (short, long) of the visually presented object seen in the mirror, and of the haptically present object felt at the end of the grasp, were always congruent; that is, when a participant contacted an object at the end of a grasp, the object was always of the same size and appeared at the same position as the object seen in the mirror. During the RNK condition, two objects were always placed, one on each side of the mirror, but if the trial was non-haptic, the object behind the mirror was subsequently removed. This was done to ensure the participant was not aurally cued to the upcoming trial type; prior work in our lab had found that participants were able to hear whether one or two objects had been initially placed, but could not hear the removal of an object after placement.

After selecting and positioning the object(s) for the current trial as indicated by the trial-order sheet, the experimenter started data collection by pressing the space-bar on the computer, which caused the Optotrack to begin recording positional data for the three IREDs, and the lenses of the goggles to become instantly transparent. The participant viewed the visually-presented object reflected in the mirror, and reached out to grasp it at the position conveyed by its virtual image at the mirror-symmetrical position behind the mirror. When the participant released the button at movement onset, the lenses of the goggles became instantly opaque, suppressing visual feedback throughout the grasp movement. After reaching, grasping, and moving a real object or pantomiming moving for an imaginary object, the participant returned their hand to its initial position and depressed the start button. The experimenter then retrieved all objects, and placed the next object(s) in position for the following trial.

Trials were administered grouped by condition. Between each condition, the participant was permitted to rest for up to 5 minutes; they were allowed to remove the goggles and to stretch their arms and hands, but they had to remain seated as the IREDs on their hand were still attached by wires to the computer. During this time, the experimenter familiarized the participant with the nature of the next condition. The experimenter also readjusted the goggles if they were uncomfortable, and provided further instruction in grasping technique to the participant if they required it.

Post data collection. After the data collection was complete, the experimenter asked the participant if they felt that they had been able to predict any of the trials in the RNK condition, and noted the response. Following this, the IREDs were removed, and the participant was compensated with $10 and signed a receipt indicating that they had been paid. The participant was offered a copy of the Letter of Information to take with them, if they wished. The experimenter also answered any questions the participant had about the aims of the study and its hypotheses, and invited the participant to be in touch by email if they wished to be informed of the results of the study after data analyses. Data collection for a single participant lasted between 45 and 60 minutes.

After collecting data for each participant, the experimenter used in-house software to view graphical representations of each grasp made by the participant (software courtesy of Dr. Robert Whitwell, University of British Columbia). The experimenter visually inspected each grasp, and compared the graphical representation of the actual grasp performed, to the trial that was supposed to be administered according to the checklist for that participant. This ensured that if the experimenter had incorrectly administered a trial but had failed to notice this during testing, that the error would be identified before data analyses began. When such a procedural error was identified, the individual trial was included for future analysis if the data observed were merely abnormal, but the trial was excluded from future analysis in cases where a wholly incorrect trial had been administered (for example, an erroneous non-haptic trial presented in the BH condition). Visual inspection of each trial also allowed the experimenter to ensure that the programs used to select individual data points for each dependent variable (such as peak grip aperture) were selecting appropriate values, and not incorrectly selecting points that were artefacts of data collection or merely local maximums. In such instances of inappropriate data selection, the experimenter adjusted the parameters of the program, and reran the program. If and only if parameter adjustment failed to select a reasonable data point, did the experimenter manually select an appropriate value. In addition, parameters for data selection were maintained largely consistent across the entire data set. These procedural standards were adopted to guard against unintentional ‘cherry picking’ of data points, and to increase the credibility of our findings in accordance with good scientific practice.

Data Analyses

Two separate four-way repeated measures Analysis of Variance (ANOVA) procedures were conducted for each of the following two dependent variables: peak hand velocity (PHV), and peak grip aperture (PGA). For each dependent variable, the first ANOVA was performed with four within-subjects factors of Presentation at 2 levels (blocked condition, randomized condition), Haptic Feedback at 2 levels (haptic trial, non-haptic trial), Object Size at 3 levels (35mm, 48mm, 60mm), and Reach Distance at 2 levels (10cm, 20cm). The second ANOVA was performed with four within-subjects factors of Knowledge at 2 levels (knowledge of upcoming haptic feedback, no knowledge of upcoming haptic feedback), Haptic Feedback at 2 levels (haptic trial, non-haptic trial), Object Size at 3 levels (35mm, 48mm, 60mm), and Reach Distance at 2 levels (10cm, 20cm). For each dependent variable, four t-tests were conducted to compare individual means: 1*a*. BH trials vs. BNH trials; 1*b*. RK haptic trials vs. RK non-haptic trials; 2*a*. RK haptic trials vs. RNK haptic trials; 2*b*. RK non-haptic trials vs. RNK non-haptic trials. All planned comparisons were conducted at $\alpha = .012$ significance ($\alpha = .05/4$, rounding down) to correct for multiple pair-wise comparisons made within each dependent variable.

Values for the third dependent variable, ‘slopes’ (a measure of grip-scaling), were obtained by averaging data across the two levels of reach distance (10cm, 20cm), and then calculating the gradient of a linear estimate of observed PGA against object size. To illustrate: three trials from a single condition that differed only by object size, but which were matched for all other independent variables, would yield three PGA values; these three values plotted on the Y-axis against the size values of the target object on the X-axis (35mm, 48mm, 60mm) would yield a line of best fit with a gradient between 0 and 1. Put another way, slopes represent the *change* in PGA divided by the *change* in target size. Steeper gradients (slopes values closer to 1) reflect a relatively greater increase in PGA as the object size increases, while shallower gradients (slopes values closer to 0) reflect relatively less increase in PGA as the object size increases. To clarify the relationship between slopes and PGA, it is helpful to note that larger slopes values reflecting a greater increase in PGA with increasing object size would also suggest a *smaller average* PGA. For example, for the smallest object (35mm), PGA during non-haptic grasps could be smaller than PGA during haptic grasps; if so, PGA for non-haptic grasps would have more room to ‘grow larger’ for grasping the largest object (60mm) than would PGA for haptic grasps, given the biomechanical constraints of the hand that limit the maximum possible grip aperture. Thus, non-haptic grasps would have a smaller *average* PGA, but a larger slopes value, whereas haptic grasps would have a larger *average* PGA, and a smaller slopes value.

Two separate two-way repeated measures ANOVAs were performed for slopes: an ANOVA with two within-subjects factors of Presentation at 2 levels (blocked condition, randomized condition), and Haptic Feedback at 2 levels (haptic trial, non-haptic trial); and an ANOVA with two within-subjects factors of Knowledge at 2 levels (knowledge of upcoming haptic feedback, no knowledge of upcoming haptic feedback), and Haptic Feedback at 2 levels (haptic trial, non-haptic trial). Four t-tests were conducted to compare individual means, making the same pair-wise comparisons as for PHV and PGA, at $\alpha = .012$ significance.

All ANOVA procedures for the dependent variables (PHV, PGA, and slopes) were conducted at $\alpha = .05$ significance. In addition, all data were corrected with the Greenhouse-Geisser epsilon multiplier, to make results more conservative.

Preliminary analyses for the fourth dependent variable, reaction time (RT), did not display common trends that emerged for other dependent variables, a finding consistent with earlier studies suggesting that the underlying processes mediating RT differ from those that mediate PHV, PGA, and slopes (Whitwell & Goodale, 2009; Tang, Whitwell, & Goodale, 2015). Consequently, RT data were excluded from further analyses and have not been reported in our results, in the interests of focusing on findings which most inform the discussion of our research question. Data from the fifth dependent variable, final grip aperture (FGA), were also excluded under similar rationale. Nonetheless, in the interests of disclosure, we have included a summary of the preliminary results for RT and FGA data in our appendices (see Appendix F).

Preliminary analyses also revealed highly similar performance between the ALT and RK conditions. Consequently, data from the ALT condition was excluded from further analysis. Data from the RK condition were selected to be included in the analyses over the ALT condition, because the RK condition allowed for direct comparison with the RNK condition, while the ALT condition did not allow for this.

The methodological rationale for experimentally manipulating object size and reach distance was to increase the ecological validity of the grasping paradigm; that is, the grasping procedures in the experiment were designed to approximate real-life grasping actions as closely as possible. However, the experiment was not designed to interpret object size and reach distance, and thus any significant effects of object size or reach distance would not necessarily allow us to draw meaningful conclusions pertaining to the hypotheses of the study. Thus, the main effects of object size and reach distance are not reported in our results, although any significant 3-way interactions involving object size or reach distance have been reported, as they may inform conclusions we draw regarding our variables of interest. Nonetheless, the ANOVAs conducted on data from PHV and PGA did include the variables ‘object size’ and ‘reach distance’, in order to account for a portion of the total variance and to increase the sensitivity of the tests. Thus, although the actual procedures conducted were four-way repeated measures ANOVAs, the results for PHV and PGA are reported in terms of two separate two-way ANOVAs: a 2x2 repeated measures ANOVA with Presentation at 2 levels (blocked condition, randomized condition), and Haptic Feedback at 2 levels (haptic trial, non-haptic trial); and a 2x2 repeated measures ANOVA with Knowledge at 2 levels (knowledge of upcoming haptic feedback, no knowledge of upcoming haptic feedback), and Haptic Feedback at 2 levels (haptic trial, non-haptic trial).

Recognizing that the experiment was designed to interpret Presentation, Haptic Feedback, and Knowledge, helps to justify the use of two *separate* ANOVAs for each dependent variable. It would not have been possible to run a single ANOVA with the aforementioned three variables all-together, as the presence of two pseudo-conditions (blocked haptic without knowledge, blocked non-haptic without knowledge) would preclude direct comparison across conditions. Thus, two ANOVAs were necessary for each dependent variable of interest. A schematic further illustrating this line of reasoning may be found in our appendices (see Appendix G).

Lastly, the given values for each dependent variable are mostly reported in the results section without accompanying units, as the following units of measurement are implied: peak hand velocity is reported in millimeters per second (mm/s); peak grip aperture is reported in millimeters (mm); and slopes have no accompanying standard unit because slopes reflect the change in peak grip aperture (measured in mm), divided by the change in target size (also measured in mm).

Results

Peak Hand Velocity (PHV)

Presentation and Haptic Feedback. No significant main effects were found for presentation, $F(1, 29) = 2.69$, $p = .112$, $\eta^2 = .085$, $1 - \beta = .354$, with mean peak hand velocity being similar for the blocked ($M = 530.45$, $SE = 17.62$) and the randomized ($M = 515.30$, $SE = 16.82$) presentation conditions. A significant main effect emerged for haptic feedback, $F(1, 29) = 66.37$, $p < .001$, $\eta^2 = .696$, $1 - \beta = 1.000$, as mean peak hand velocity was faster for haptic grasps ($M = 552.51$, $SE = 17.47$) than for non-haptic grasps ($M = 493.24$, $SE = 16.50$). An interaction emerged between presentation and haptic feedback, $F(1, 29) = 16.98$, $p < .001$, $\eta^2 = .369$, $1 - \beta = .978$, as haptic grasps were more susceptible to the influence of presentation than were non-haptic grasps: peak hand velocity for haptic grasps was faster in the blocked condition than in the randomized condition, whereas non-haptic grasps differed less between the blocked condition and the randomized condition.

Planned comparisons between group means revealed that within the blocked condition, haptic grasps ($M = 572.92$, $SE = 19.36$) displayed significantly faster peak hand velocities than non-haptic grasps ($M = 487.98$, $SE = 18.02$), $t(29) = 6.78$, $p < .001$. The same was true for the randomized condition, where haptic grasps ($M = 532.09$, $SE = 17.29$) also showed significantly faster peak hand velocities than non-haptic grasps ($M = 498.51$, $SE = 16.75$), $t(29) = 6.53$, $p < .001$, (see Figure 1).

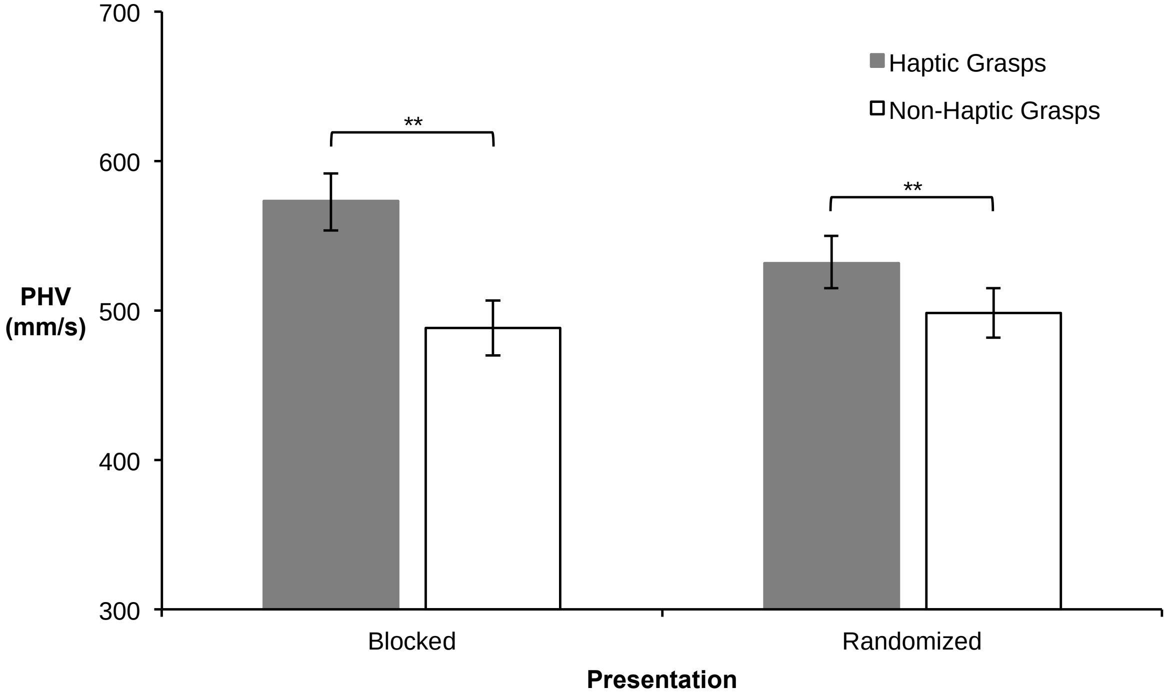

Figure 1. Mean values for peak hand velocity (PHV), in mm/s, displayed by presentation and haptic feedback. Blocked presentation refers to data from the BH condition for haptic grasps, and data from the BNH condition for non-haptic grasps. Randomized presentation refers to data from the RK condition, in which haptic grasps reflect extracted haptic trials, and non-haptic grasps reflect extracted non-haptic trials. Brackets between group means indicate planned comparisons revealing significant differences at * $p < .012$, and ** $p \leq .001$. Error bars represent standard error.

Knowledge and Haptic Feedback. No significant main effects were found for knowledge of upcoming haptic feedback, *F*(1, 29) = 2.41, *p* = .132, η^2 = .077, 1 - β = .323, with similar mean peak hand velocities between the RK condition (*M* = 515.30, *SE* = 16.82) and the RNK condition (*M* = 528.04, *SE* = 19.40). A significant main effect emerged for haptic feedback, *F*(1, 29) = 33.27, *p* < .001, η^2 = .534, 1 - β = 1.000, as mean peak hand velocity was faster for haptic grasps (*M* = 528.60, *SE* = 17.69) than for non-haptic grasps (*M* = 514.74, *SE* = 17.76). An interaction emerged between haptic feedback and knowledge of upcoming haptic feedback, *F*(1, 29) = 34.30, *p* < .001, η^2 = .542, 1 - β = 1.000, as non-haptic grasps were more susceptible to the influence of knowledge than were haptic grasps: peak hand velocity for non-haptic grasps was slower in the RK condition than in the RNK condition, whereas haptic grasps were similar across the RK and RNK conditions. In addition, a 3-way interaction emerged between haptic feedback, object size, and reach distance, *F*(2, 57) = 3.34, *p* = .044, η^2 = .103, 1 - β = .600, a finding which will be returned to in the discussion section (see Table 1).

Planned comparisons between group means revealed no significant differences in peak hand velocity between haptic grasps in the RK condition (*M* = 532.09, *SE* = 17.29) and haptic grasps in the RNK condition (*M* = 525.11, *SE* = 18.72), *t*(29) = 1.02, *p* = .316. Non-haptic grasps, however, were significantly slower in the RK condition (*M* = 498.51, *SE* = 16.75) than in the RNK condition (*M* = 530.96, *SE* = 20.14), *t*(29) = 3.09, *p* = .004, (see Figure 2).

Peak Grip Aperture (PGA)

Presentation and Haptic Feedback. No significant main effects were found for presentation, *F*(1, 29) = 3.24, *p* = .082, η^2 = .100, 1 - β = .413, with mean peak grip aperture being similar for the blocked (*M* = 83.50, *SE* = 1.27) and the randomized (*M* = 85.43 *SE* = 1.75) presentation conditions. A significant main effect emerged for haptic feedback, *F*(1, 29) = 6.89,

Table 1

Peak Hand Velocity (PHV) values by Haptic Feedback, Object Size, and Reach Distance

		Object Size		
		35	48	60
Near Reach	Haptic	465.67 (16.59)	477.90 (16.67)	473.52 (17.68)
	Non-Haptic	456.58 (18.83)	451.98 (16.25)	454.95 (17.88)
	Difference	9.09	25.92	18.57
Far Reach	Haptic	583.54 (20.79)	580.15 (20.82)	590.83 (21.25)
	Non-Haptic	569.30 (21.69)	575.79 (20.10)	579.81 (21.02)
	Difference	14.24	4.36	11.02

Note. Mean values for peak hand velocity, in mm/s, summed across RK and RNK conditions. Standard error is displayed in brackets. The near reach distance was 10cm; the far reach distance was 20cm. Object sizes in mm.

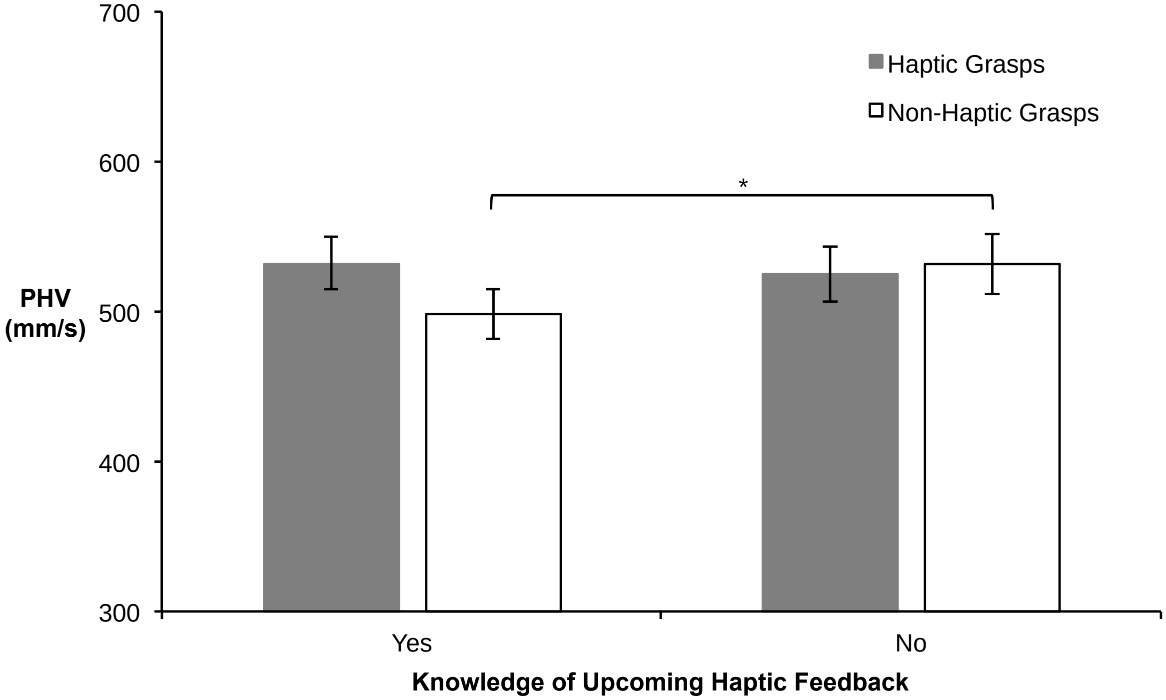

Figure 2. Mean values for peak hand velocity (PHV), in mm/s, displayed by haptic feedback and knowledge of upcoming haptic feedback. Under knowledge of upcoming haptic feedback, ‘Yes’ refers to data from the RK condition, and ‘No’ refers to data from the RNK condition. Haptic grasps and non-haptic grasps correspond to haptic and non-haptic trials extracted from within each condition. Brackets between group means indicate planned comparisons revealing significant differences at * $p < .012$, and ** $p \leq .001$. Error bars represent standard error.

p = .014, η^2 = .192, 1 - β = .718, as mean peak grip aperture was greater for haptic grasps (*M* = 86.80, *SE* = 1.28) than for non-haptic grasps (*M* = 82.12, *SE* = 2.01). No interaction emerged between presentation and haptic feedback, *F*(1, 29) = 3.65, *p* = .066, η^2 = .112, 1 - β = .455. However, a 3-way interaction emerged between presentation, haptic feedback, and object size, *F*(2, 57) = 5.55, *p* = .007, η^2 = .161, 1 - β = .828, a finding which will be interpreted in the discussion section (see Table 2).

Planned comparisons between group means revealed no significant differences in peak grip aperture for the blocked condition between haptic grasps (*M* = 86.77, *SE* = 1.31) and non-haptic grasps (*M* = 80.22, *SE* = 2.19), *t*(29) = 2.54, *p* = .017. Likewise, no significant differences emerged in the randomized condition between haptic grasps (*M* = 86.83, *SE* = 1.66) and non-haptic grasps (*M* = 84.03, *SE* = 2.06), *t*(29) = 2.20, *p* = .036, (see Figure 3).

Knowledge and Haptic Feedback. A significant main effect emerged for knowledge of upcoming haptic feedback, *F*(1, 29) = 9.08, *p* = .005, η^2 = .238, 1 - β = .829, with a lower mean peak grip aperture in the RK condition (*M* = 85.43, *SE* = 1.75) than in the RNK condition (*M* = 89.01, *SE* = 1.78). A significant main effect emerged for haptic feedback, *F*(1, 29) = 5.23 *p* = .030, η^2 = .153, 1 - β = .599, as mean peak grip aperture was greater for haptic grasps (*M* = 87.94, *SE* = 1.65) than for non-haptic grasps (*M* = 86.50, *SE* = 1.73). An interaction emerged between haptic feedback and knowledge of upcoming haptic feedback, *F*(1, 29) = 4.31, *p* = .047, η^2 = .129, 1 - β = .518, as non-haptic grasps were more susceptible to the influence of knowledge than haptic grasps. Non-haptic grasps showed increased peak grip aperture when knowledge was unavailable, whereas haptic grasps were unaffected. A 3-way interaction also emerged between knowledge of upcoming haptic feedback, haptic feedback, and object size, *F*(2, 57) = 15.31, *p* < .001, η^2 = .346, 1 - β = .999, which will be interpreted in the discussion section (see Table 3).

Table 2

Peak Grip Aperture (PGA) values by Presentation, Haptic Feedback, and Object Size

		Object Size		
		35	48	60
Blocked	Haptic	82.04 (1.39)	86.72 (1.36)	91.55 (1.54)
	Non-Haptic	71.83 (2.79)	79.62 (2.32)	89.21 (1.86)
	Difference	10.21	7.10	2.34
Randomized	Haptic	80.23 (1.91)	87.56 (1.71)	92.71 (1.65)
	Non-Haptic	76.32 (2.43)	83.30 (2.28)	92.47 (1.83)
	Difference	3.91	4.26	0.24

Note. Mean values for peak grip aperture, in mm, summed across reach distance (near, far). Standard error is displayed in brackets. Randomized refers to data from the RK condition. Object sizes in mm.

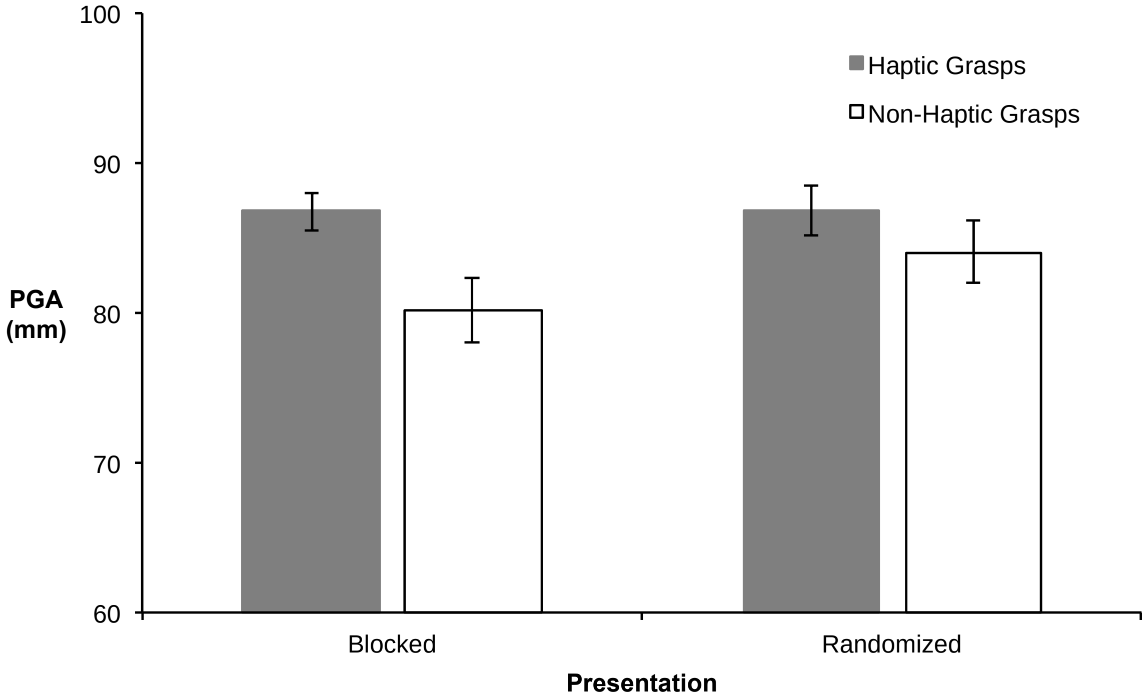

Figure 3. Mean values for peak grip aperture (PGA), in mm, displayed by presentation and haptic feedback. Blocked presentation refers to data from the BH condition for haptic grasps, and data from the BNH condition for non-haptic grasps. Randomized presentation refers to data from the RK condition, in which haptic grasps reflect extracted haptic trials, and non-haptic grasps reflect extracted non-haptic trials. Planned comparisons did not reveal any significant differences between group means at $p < .012$. Error bars represent standard error.

Table 3

Peak Grip Aperture (PGA) values by Knowledge, Haptic Feedback, and Object Size

		Object Size		
		35	48	60
Knowledge	Haptic	80.23 (1.91)	87.56 (1.71)	92.71 (1.65)
	Non-Haptic	76.32 (2.43)	83.30 (2.28)	92.47 (1.83)
	Difference	3.91	4.26	0.24
No Knowledge	Haptic	83.45 (1.96)	88.90 (1.80)	94.80 (1.83)
	Non-Haptic	84.59 (1.83)	88.79 (1.91)	93.54 (1.92)
	Difference	-1.14	0.11	1.26

Note. Mean values for peak grip aperture, in mm, summed across reach distance (near, far). Standard error is displayed in brackets. Knowledge refers to knowledge of upcoming haptic feedback. Object sizes in mm.

Planned comparisons between group means revealed no significant differences in peak grip aperture between haptic grasps in the RK condition ($M = 86.83$, $SE = 1.66$) and haptic grasps in the RNK condition ($M = 89.05$, $SE = 1.78$), $t(29) = 2.35$, $p = .025$. Non-haptic grasps, however, showed significantly smaller peak grip apertures in the RK condition ($M = 84.03$, $SE = 2.06$) than in the RNK condition ($M = 88.97$, $SE = 1.78$), $t(29) = 2.95$, $p = .006$, (see Figure 4).

Slopes

Presentation and Haptic Feedback. No significant main effects were found for presentation, $F(1, 29) = 2.90$, $p = .099$, $\eta^2 = .091$, $1 - \beta = .377$, with slopes being similar for the blocked ($M = .537$, $SE = .041$) and the randomized ($M = .572$, $SE = .037$) presentation conditions. A significant main effect emerged for haptic feedback, $F(1, 29) = 21.68$, $p < .001$, $\eta^2 = .428$, $1 - \beta = .994$, as slopes were steeper for non-haptic grasps ($M = .669$, $SE = .053$) than for haptic grasps ($M = .440$, $SE = .034$). An interaction emerged between presentation and haptic feedback, $F(1, 29) = 10.68$, $p = .003$, $\eta^2 = .269$, $1 - \beta = .885$, as haptic grasps were more susceptible to the influence of presentation than were non-haptic grasps: within both the blocked condition and the randomized condition, slopes for non-haptic grasps appeared to be steeper than for haptic grasps, although this difference between non-haptic and haptic grasps was greater in the blocked condition than in the randomized condition.

Planned comparisons between group means revealed that within the blocked condition, slopes for non-haptic grasps ($M = .694$, $SE = .063$) were significantly steeper than for haptic grasps ($M = .380$, $SE = .039$), $t(29) = 4.71$, $p < .001$. The same was true for the randomized condition, where non-haptic grasps ($M = .645$, $SE = .048$) also showed significantly steeper slopes than haptic grasps ($M = .500$, $SE = .036$), $t(29) = 3.46$, $p = .002$, (see Figure 5).

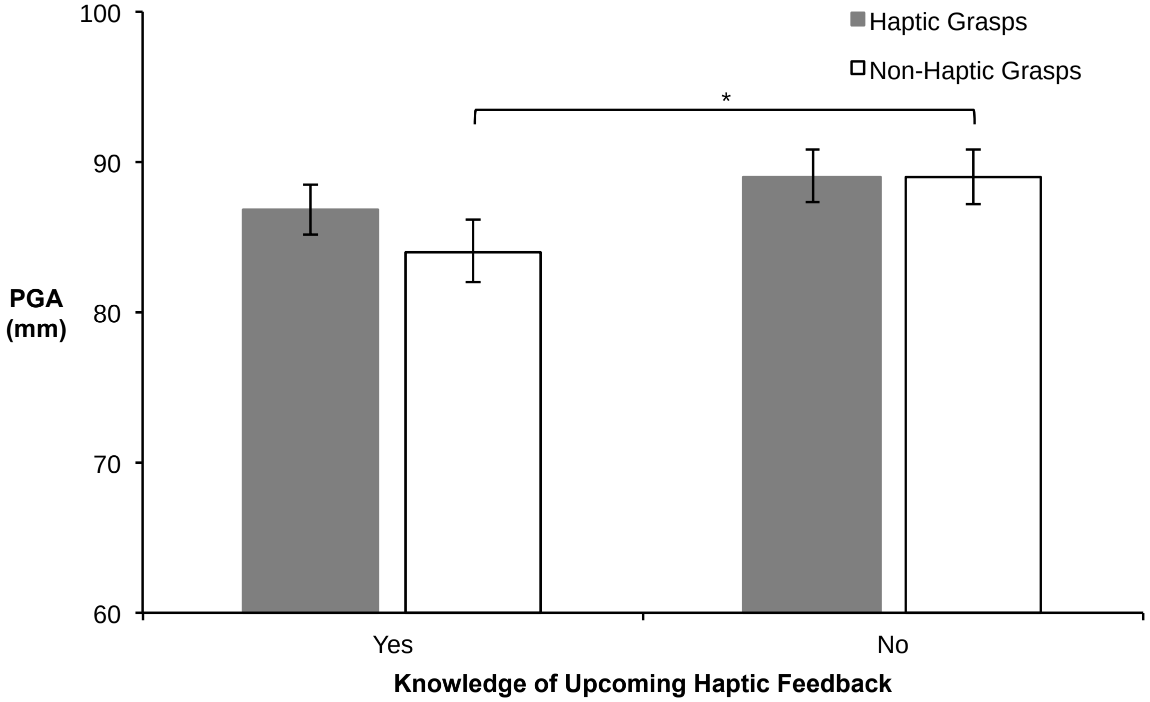

Figure 4. Mean values for peak grip aperture (PGA), in mm, displayed by haptic feedback and knowledge of upcoming haptic feedback. Under knowledge of upcoming haptic feedback, 'Yes' refers to data from the RK condition, and 'No' refers to data from the RNK condition. Haptic grasps and non-haptic grasps correspond to haptic and non-haptic trials extracted from within each condition. Brackets between group means indicate planned comparisons revealing significant differences at * $p < .012$, and ** $p \leq .001$. Error bars represent standard error.

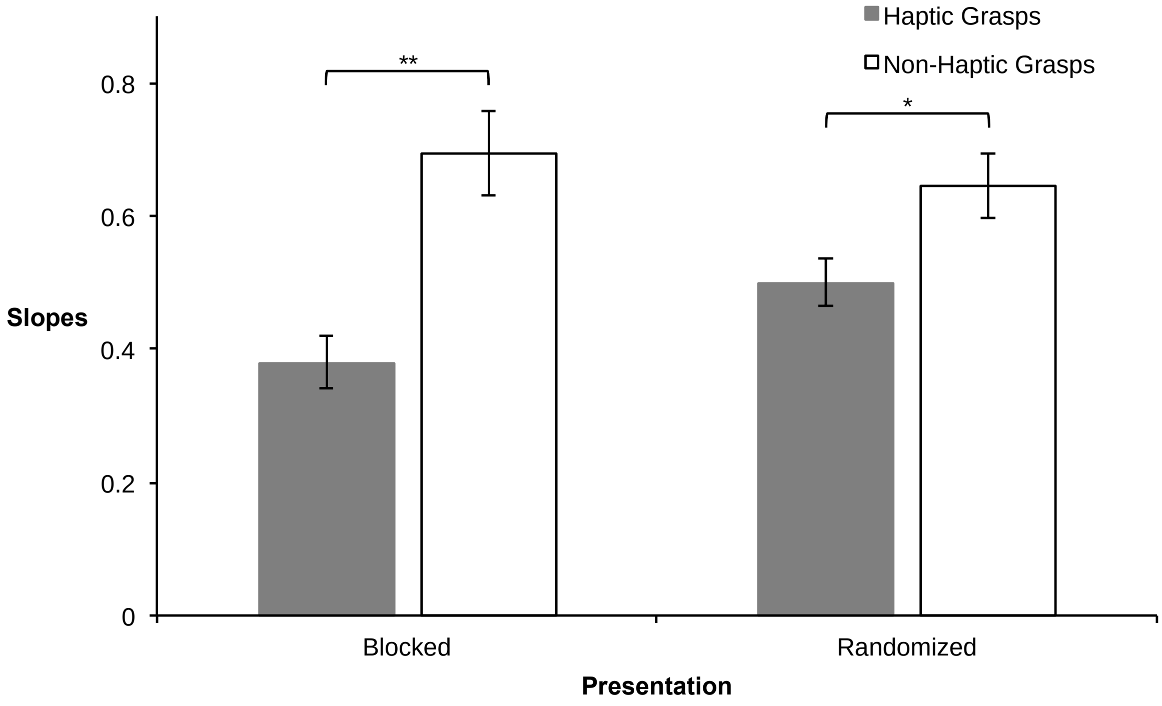

Figure 5. Mean values for slopes (the change in peak grip aperture divided by the change in target size), displayed by presentation and haptic feedback. Blocked presentation refers to data from the BH condition for haptic grasps, and data from the BNH condition for non-haptic grasps. Randomized presentation refers to data from the RK condition, in which haptic grasps reflect extracted haptic trials, and non-haptic grasps reflect extracted non-haptic trials. Brackets between group means indicate planned comparisons revealing significant differences at * $p < .012$, and ** $p \leq .001$. Error bars represent standard error.

Knowledge and Haptic Feedback. A significant main effect emerged for knowledge of upcoming haptic feedback, $F(1, 29) = 34.95$, $p < .001$, $\eta^2 = .547$, $1 - \beta = 1.000$, with steeper slopes in the RK condition ($M = .572$, $SE = .037$) than in the RNK condition ($M = .406$, $SE = .032$). No significant main effect emerged for haptic feedback, $F(1, 29) = 0.762$, $p = .390$, $\eta^2 = .026$, $1 - \beta = .135$, as slopes were similar between non-haptic grasps ($M = .501$, $SE = .038$) and haptic grasps ($M = .477$, $SE = .030$). An interaction emerged between haptic feedback and knowledge of upcoming haptic feedback, $F(1, 29) = 28.91$, $p < .001$, $\eta^2 = .499$, $1 - \beta = .999$, as non-haptic grasps were more susceptible to the influence of knowledge than were haptic grasps: slopes for non-haptic grasps appeared to be steeper in the RK condition than in the RNK condition, whereas slopes for haptic grasps differed very little between the RK and RNK conditions.

Planned comparisons between group means revealed no significant differences in slopes between haptic grasps in the RK condition ($M = .500$, $SE = .036$) and haptic grasps in the RNK condition ($M = .454$, $SE = .032$), $t(29) = 1.48$, $p = .150$. Non-haptic grasps, however, showed significantly steeper slopes in the RK condition ($M = .645$, $SE = .048$) than in the RNK condition ($M = .358$, $SE = .038$), $t(29) = 7.16$, $p < .001$, (see Figure 6).

Our initial findings appeared to indicate a surprising difference between haptic and non-haptic grasps in the RNK condition, only for the dependent variable ‘slopes’. Accordingly, a post-hoc two-sample t-test was conducted at $\alpha = .012$ significance, revealing that slopes for haptic grasps in the RNK condition ($M = .454$, $SE = .032$) were significantly steeper than slopes for non-haptic grasps in the RNK condition ($M = .358$, $SE = .038$), $t(29) = 3.42$, $p = .002$, (see Figure 6). The implications and the possible cause of this highly unexpected result are explored in the discussion section.

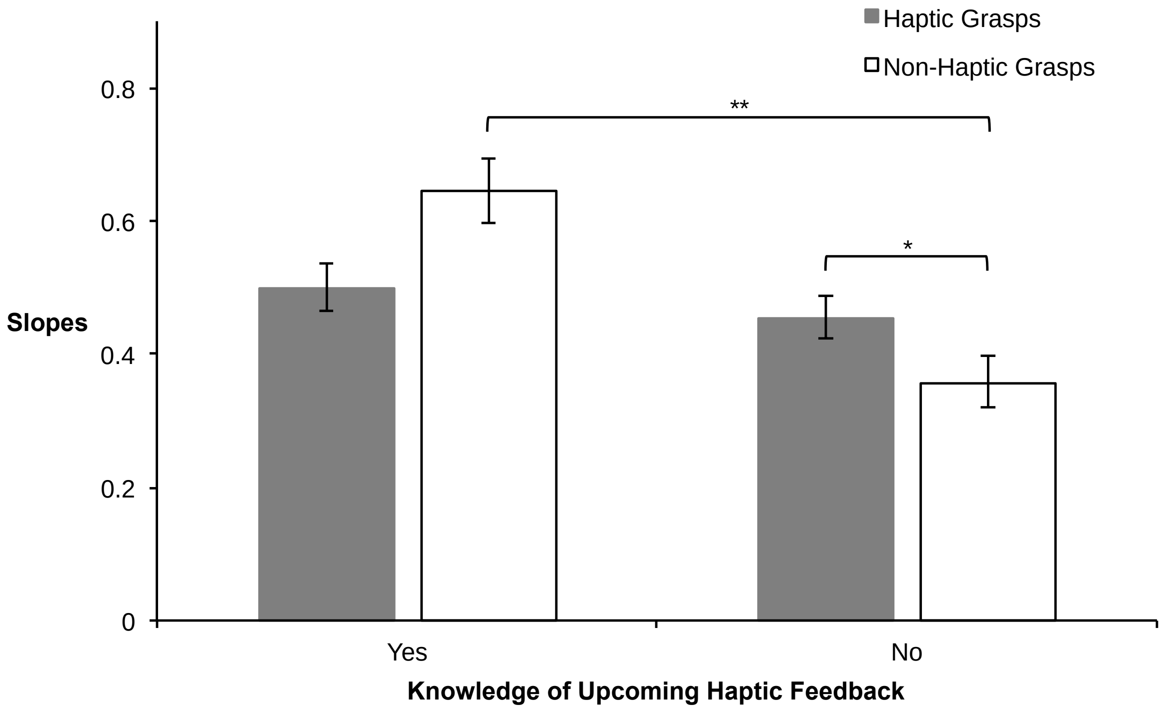

Figure 6. Mean values for slopes (the change in peak grip aperture divided by the change in target size), displayed by haptic feedback and knowledge of upcoming haptic feedback. Under knowledge of upcoming haptic feedback, ‘Yes’ refers to data from the RK condition, and ‘No’ refers to data from the RNK condition. Haptic grasps and non-haptic grasps correspond to haptic and non-haptic trials extracted from within each condition. Brackets between group means indicate comparisons revealing significant differences at: * $p < .012$; ** $p \leq .001$. Error bars represent standard error.

Discussion

The current study made three hypotheses, which are restated here and will each be addressed in turn. The hypotheses were: (1) When controlling for knowledge, interleaving haptic and non-haptic trials will not result in natural prehension on the non-haptic trials; (2) Non-haptic (pantomime) grasps will be susceptible to knowledge of upcoming haptic feedback, whereas haptic (normal) grasps will not be; (3) Pantomime grasps will show decrements in precision and differences in several kinematic variables compared to normal grasps.

Interleaving Haptic and Non-Haptic Trials Does Not Normalize Non-Haptic Grasps

Our first hypothesis, that interleaved haptic and non-haptic trials will not result in natural prehension on the non-haptic trials, is supported by our finding that in the RK condition, haptic grasps differ from non-haptic grasps for both PHV and slopes. The CSH would predict no such difference, as Bingham *et al*. (2007) reported no differences between haptic and non-haptic grasps in their randomized condition. But Bingham and colleagues neglected to control for knowledge, making their randomized condition the equivalent of our RNK condition – and this is indeed what we find: no differences between haptic and non-haptic grasps in the RNK condition, at least for PHV and PGA. That a difference exists for slopes is somewhat perplexing, and will be discussed later, but it does not weaken our finding that, when controlling for knowledge, interleaving haptic and non-haptic trials does *not* normalize prehension on the non-haptic trials.

Additional support for our first hypothesis comes from the emergence of a main effect of knowledge for both PGA and slopes. The CSH maintains that manual prehension is shaped by past haptic feedback, and thus would predict no differences between our RK and RNK conditions, which are identical in terms of haptic feedback across trials (having the same sequence of haptic and non-haptic trials). However, we find differences for PGA and slopes, suggesting that knowledge of upcoming haptic feedback can influence manual prehension. Moreover, no main effects of presentation emerged for any of the three dependent variables – this observation, juxtaposed against emergent main effects of knowledge, suggests that knowledge of future haptic feedback is a far more potent force in shaping current manual prehension than is the tactile experience of past haptic feedback. In summary, these findings provide strong support for our initial contention that the natural prehension observed by Bingham *et al*. during interleaved haptic and non-haptic trials was indeed being driven by an effect of knowledge (in that case, an *absence* of knowledge), rather than by intermittent haptic feedback. Were the natural prehension being driven by intermittent haptic feedback, rather than by knowledge, then no differences would have emerged between our RK and RNK conditions, which was not the case.

Pantomime Grasps are Susceptible to Knowledge, Normal Grasps are Unsusceptible

Our second hypothesis, that non-haptic (pantomime) grasps will be susceptible to knowledge of upcoming haptic feedback whereas haptic (normal) grasps will not be, is strongly supported by our results. Before presenting our argument, let us briefly recall that pantomime grasps have slower peak hand velocity, smaller peak grip aperture, and show less grip scaling than normal grasps (among other variables; Goodale *et al*., 1994). Returning to our data, we find that across all three dependent variables (PHV, PGA, and slopes), there is a difference between non-haptic grasps in the RK and RNK conditions, indicating that pantomime grasps are influenced by knowledge of upcoming haptic feedback. Moreover, across all three dependent variables, we find *no* differences between haptic grasps in the RK and RNK conditions, suggesting that normal grasps are unaffected by the influence of knowledge of upcoming haptic feedback. These two findings also appear to be driving the interaction between haptic feedback and knowledge of upcoming haptic feedback which emerges for all three dependent variables.

Support for our second hypothesis in turn supports the idea that the dorsal stream is cognitively inaccessible, whereas the ventral stream is cognitively accessible – a finding that aligns with prior studies exploring this phenomenon (Westwood *et al*., 2000; Whitwell *et al*., 2008). Haptic grasps, which are normal grasps driven by the dorsal stream, were unaffected by cognitively available information such as knowledge of upcoming haptic feedback. Conversely, non-haptic grasps, which are pantomime grasps driven by the ventral stream, were susceptible to knowledge of upcoming haptic feedback… Or were they?

While the susceptibility of non-haptic grasps to the effect of knowledge is evident from our results, we contend that it is incorrect to refer to this effect as a susceptibility of pantomime (and therefore ventral-stream driven) grasps. Here, differentiating the nuances of the terminology is critical to properly conveying our result. We have used the term ‘pantomime grasp’ to refer to a ventral-stream mediated process, and we have also used the terms ‘pantomime grasp’ and ‘non-haptic grasp’ interchangeably, as being essentially the same thing. However, in cases where there is *no* knowledge of upcoming haptic feedback, as in our RNK condition, we hold that non-haptic grasps do not constitute ‘pantomime grasps’, as they do not show grasp kinematics characteristic of a ventral-stream-mediated process – at least, they are not ‘pantomime grasps’ according to the defining features of pantomime grasps mentioned earlier. We argue that such no-knowledge non-haptic grasps do not appear like true pantomime grasps because they are not being driven by the ventral stream – rather, they are being driven by the dorsal stream. Our results support such a conclusion: the similarities, across all three dependent variables (excepting the slopes RNK condition), between the *three* groups – haptic trials in the RK condition, haptic trials in the RNK condition, and non-haptic trials in the RNK condition – suggest that these three groups are all being driven by the dorsal stream; the difference between these three groups on the one hand, and non-haptic trials in the RK condition on the other hand, suggests that by contrast, only non-haptic trials in the RK condition are being driven by the ventral stream.

To present this from another angle, we may characterize the observed effect (of non-haptic grasp susceptibility to knowledge, and haptic grasp unsusceptibility) as being driven by two components. Firstly, haptic and non-haptic grasps differ in the RK condition because they are being driven by two different systems – the dorsal and ventral streams respectively. Secondly, non-haptic grasps differ between the RK and RNK conditions because they are also being driven by two different systems – the ventral and dorsal streams respectively. In short, denying knowledge of upcoming haptic feedback provokes a shift away from using the ventral stream for non-haptic grasps, instead employing the dorsal stream.

In summary, our results suggest the following: when there is knowledge of upcoming haptic feedback (as in our RK condition) haptic grasps are dorsal-stream driven, and non-haptic grasps are ventral-stream driven; when there is no knowledge of upcoming haptic feedback (as in our RNK condition) both haptic and non-haptic grasps are dorsal-stream driven.

Note that our results are consistent with the explanation, first proffered by the anonymous reviewer, for the natural prehension observed by Bingham *et al*. (2007) during interleaved haptic and non-haptic grasps: without knowledge of upcoming haptic feedback, as in Bingham's randomized condition and our RNK condition, the visual system engages the dorsal stream for *both* haptic and non-haptic grasps.

Such an explanation is also intuitive and logical: given that participants do not know until the *end* of the grasp whether the grasp was haptic or non-haptic, there should be no differences for in-flight grasp kinematics between haptic and non-haptic grasps, which is indeed what we observe in our RNK condition for PHV and PGA. Extending this line of reasoning, the most plausible explanation for similar grasp kinematics across different types of grasps is mediation by a common system, such as the dorsal stream. Here, the similarities between groups discussed earlier support the idea that the system responsible for these common characteristics is indeed the dorsal stream, and not the ventral stream.

Another line of reasoning in support of this conclusion comes from consideration of task incentives. In the RNK condition, for all trials – haptic and non-haptic – the incentive is not to be ‘lazy’. An error made during a grasp in which an object is prepared for but no object is encountered is not as serious as an error made during a grasp in which no object is prepared for but an object is encountered. As Whitwell *et al*. (2015) pointed out, the assured removal of haptic feedback (as in our BNH condition) changes task incentives because there is no longer any consequence of a poorly-performed grasp. But when haptic feedback is only *possibly* removed, as in our RNK condition, the undesirable consequences of a poorly-performed grasp (such as knocking over the object) remain. The dorsal stream is known to be recruited when there is incentive to perform a precise grasp due to *guaranteed* undesirable consequences. Thus, when there is incentive to perform a precise grasp because of the *possible* (and in this case, also *likely*) undesirable consequences of not doing so, it seems probable that the dorsal stream is also recruited.

Lastly, our claim that the dorsal stream mediates both haptic and non-haptic grasps in our RNK condition rests upon the assumption that the dorsal stream is *capable* of mediating grasps in which haptic feedback is denied. Indeed, Bingham *et al*.’s (2007) initial criticism of the TVSH rested upon their finding of natural prehension in what was essentially a RNK condition, and their subsequent conclusion that the dorsal stream could support pantomime (non-haptic) grasping – supposedly contrary to the TVSH model in which non-haptic grasps are mediated by the ventral stream, not the dorsal stream. However, the claim that the dorsal stream can mediate even non-haptic grasps is not contentious. In their original study of patient DF, Goodale and colleagues (1991) reported that DF could accurately modulate the orientation of her hand to post a card through an *imagined* slot. Later studies corroborated this earlier report, finding that DF showed preserved grip scaling when reaching to familiar, but *imagined* objects (Goodale *et al*., 1994). This suggests that the dorsal stream may be capable of mediating grasps even when haptic feedback in known to be absent, and that the mechanisms regulating the recruitment of the dorsal versus the ventral stream may be more heavily influenced by the intended purpose of the grasp than by knowledge of upcoming haptic feedback. Indeed, there is much support for the idea that the intentions behind our grasps influence how we approach an object when we pick it up (Rosenbaum, Meulenbroek, Vaughan, & Jansen, 2001). Regardless, it seems that there is support for the idea that absence of haptic feedback does not *preclude* dorsal-stream mediation of grasping actions.

In summary, we argue that both our data and consideration of task incentives support the conclusion that in the absence of knowledge of upcoming haptic feedback, grasps are mediated by the dorsal stream. From this basis, our data lead us to conclude that normal grasps are immune to knowledge of upcoming haptic feedback, whereas pantomime grasps (or more accurately, *ventral-stream driven grasps*) are susceptible to such knowledge.

Of course, the one finding that appears to run counter to this conclusion is the surprising emergence of a difference in slopes between haptic and non-haptic trials in our RNK condition. Because this contrary finding has implications for all three of our hypotheses, we explore it in detail after this preliminary discussion of our main results, and we include an argument for why such a seemingly contrary finding may not necessarily weaken the conclusions we have drawn here regarding our second hypothesis.

Pantomime Grasps are Less Precise than Normal Grasps

Our third hypothesis, that pantomime grasps will show decrements in precision and differences in several kinematic variables compared to normal grasps, is supported by our findings that BH grasps (normal grasps) differ from BNH grasps (pantomime grasps) for both PHV and for slopes. Specifically, pantomime grasps had slower peak hand velocities, suggesting that participants were less confident in performing these grasps, a finding consistent with Bingham *et al*. (2007). Pantomime grasps also showed larger values for slopes, indicating that participants were less precise in their execution of pantomime grasps, as their peak grip apertures varied more widely across the different sizes of target objects for pantomime grasps than for normal grasps. Our specific prediction that BH and BNH conditions would differ on all five dependent variables was partially supported, given that two of the three dependent variables we analyzed conformed to this predication, with PGA being the notable exception. Our specific prediction that for slopes, the difference between the BH and BNH conditions would be greater than for any other pair-wise comparison of haptic and non-haptic trials, was fully supported, with the greatest effect size comparing haptic and non-haptic trials emerging from the difference between the BH and BNH conditions.

Compelling support for our third hypothesis also comes from the emergence of a main effect for haptic feedback in five of the six ANOVAs conducted, with only the slopes analysis of Knowledge and Haptic Feedback not showing this effect, a result which is likely being driven by the peculiar difference between haptic and non-haptic trials in the RNK condition. Thus, consistent with several prior studies (Bingham *et al*., 2007; Goodale *et al*., 1994; Westwood *et* *al.*, 2000), normal grasps differ from pantomime grasps on kinematic variables such as PHV, PGA, and slopes. In short, when one *has* knowledge of upcoming haptic feedback, grasps require a tangible end-point in order to retain natural prehension. These findings also appear to be driving the interactions between presentation and haptic feedback that emerged for PHV and for slopes.

Interpreting the 3-way Interactions

Although our experiment was not designed to interpret the effects of object size or reach distance on grasp kinematics, examining the three significant 3-way interactions may nonetheless be informative. Of greatest interest is the interaction that emerged for PGA between haptic feedback, knowledge of upcoming haptic feedback, and object size. Peak grip aperture increases as object size increases, and this increase is greater for non-haptic grasps than for haptic grasps, but only when participants have knowledge of upcoming haptic feedback. When participants have no knowledge, the increase in PGA with increasing target size does not differ between haptic and non-haptic grasps (as one would expect, since participants don't know whether the upcoming grasp will be haptic or non-haptic).

Interestingly, we see practically this same result in our slopes data, which is hardly surprising given that slopes represent peak grip aperture as a function of target size. For comparison, our observed greater increase in PGA for non-haptic grasps as target size increases is also reflected by a much larger slopes value in the blocked non-haptic condition than in the blocked haptic condition. Additionally, the 3-way interaction for PGA mentioned here mirrors the 2-way interaction between haptic feedback and knowledge of upcoming haptic feedback that emerged for slopes. These significant results are related because they all involve the same variables and only those variables. Such converging evidence from the 3-way interaction is still useful, however, as it strengthens our associated findings for slopes.

Examining this 3-way interaction for PGA also allows us to draw three interesting inferences about our experimental procedure. Firstly, for non-haptic grasps with knowledge, the increase in PGA as target size increases provides evidence that participants were complying with instructions – that is, they were actually opening their hand wider as target size increased, even though there was no consequence of not doing so. Participants had the option of being 'lazy', and simply using a small grasp for all sizes of the visually-presented non-haptic object, but the interaction data nicely illustrates that they did not do so (see Table 3).

Secondly, the knowledge component driving the 3-way interaction, namely that the increase in PGA with increasing target size is similar for haptic and non-haptic grasps in the no-knowledge condition, suggests that participants were unable to predict whether upcoming trials would be haptic or non-haptic in our RNK condition.

Thirdly, the similarity in PGA between haptic and non-haptic grasps in the knowledge condition for the largest object size (60mm) suggests that for grasping objects of that size, participants were running up against anatomical constraints of the hand that limit the maximum possible grip aperture. This is useful information, as it informs our future experiments and suggests that when employing normal and pantomime grasps to explore grasp kinematics for dorsal-stream and ventral-stream mediated actions, consideration should be given to the size of target objects, lest ceiling effects limit the extent to which normal and pantomime grasps will differ on dependent variables such as PGA. It is particularly interesting to note that such ceiling effects still affect the non-haptic (with knowledge) grasps, despite these grasps appearing to have a lower average PGA than haptic grasps. That is, despite smaller non-haptic objects appearing to evoke slightly ‘lazy’ or possibly just inaccurate grasps, the largest non-haptic object appeared not to evoke a similarly ‘lazy’ or inaccurate response (see Table 3).

The second 3-way interaction for PGA involved presentation, haptic feedback, and object size. Here, haptic grasps elicit larger peak grip apertures than non-haptic grasps, but the difference in peak grip aperture between haptic and non-haptic grasps decreases as object size increases. Moreover, the absolute differences *and* the decrease in difference with increasing object size was smaller in the randomized condition than in the blocked condition (see Table 2). The first observation presumably reflects the increasing influence of anatomical constraints on grip aperture as the grasps approach maximal grip aperture. The fact that this effect was mediated by presentation suggests an influence of trial-history based on the past regularity of haptic feedback, a plausible notion given that prior studies support the idea that the primary determinant of visual-system-mediated prehension *besides* visual input, is recent proprioceptive and tactile information – i.e. what happened on the last trial (Tang, Whitwell, & Goodale, 2015; Whitwell, Lambert, & Goodale, 2008). However, despite the significant interaction, we can provide little further explanation as our experiment lacks the power to meaningfully interpret this result.

The third 3-way interaction emerged for PHV and involved haptic feedback, object size, and reach distance. Peak hand velocity is higher for haptic grasps than for non-haptic grasps (indicated by faster peak hand velocities for haptic grasps in both the BH and RK conditions). In addition, the degree to which PHV is higher for haptic grasps appears to *increase* with increasing object size when the object is *near*, and to *decrease* with increasing object size when the object is *far* (see Table 1). However, given that this interaction involves both object size and reach distance, we can do little to interpret it beyond noting that the effect size is small (η^2 = .103), and that it does not appear to compromise any results from our 2-way interactions.

Why Haptic and Non-Haptic Slopes Differ in the RNK condition

As mentioned previously, preliminary results pointed to a difference between haptic and non-haptic trials in the RNK condition for the variable ‘slopes’ – a difference which a post-hoc test found to be significant. This finding is not merely remarkable because no such differences were found for PHV or PGA, it is remarkable because it indicates that participants exhibited different grip scaling (slopes values) for haptic versus non-haptic trials, despite having no knowledge of whether the grasp they were currently performing was a haptic or a non-haptic grasp. It appears as if the participant’s hand had knowledge of the state of upcoming haptic feedback for the current grasp, but their brain did not. What was happening? Were the participants psychics? This one finding ran counter to all our other results, and required an explanation.

The first clue to the probable mechanism arises from recognizing that while haptic and non-haptic trials differ in the RNK condition for slopes, they do not differ at all for PGA. This observation guides our reasoning with regard to the mechanism behind the effect – it suggests that whatever is causing the difference is having a uniform effect on both the haptic and the non-haptic trials, irrespective of any other features of the trial. Put another way, the mechanism is affecting the peak grip aperture as a function of target size, without affecting peak grip aperture. Because the mean peak grip aperture does not differ between haptic and non-haptic trials in the RNK condition, the mechanism that causes the effect for slopes must be acting on the ‘as a function of target size’ aspect, suggesting that the PGA is actually varying *consistently* as a function of something else, which only incidentally happens to correspond to the pattern of haptic and non-haptic trials. This explanation is reassuring and also parsimonious, since it does not rely on the highly unlikely premise that participants are somehow (consciously or unconsciously) predicting the state of haptic feedback on upcoming trials in the RNK condition.

Building on this explanation leads us to consider what factors might be responsible for the effect, and a likely candidate emerges: trial history. Trial history is known to influence dorsal-stream mediated grasping, it is known to act independently of the effect of any knowledge of visual feedback availability on future grasps, and it is known that the strength of its effect varies as a function of time since the past actions which cause the effect actually occurred, making it a viable candidate for something that varies across multiple trials while exerting its strongest effect based on the most recent trial (Whitwell *et al.*, 2008). But if trial history is the culprit, then what is the ‘murder-weapon’? Or rather, if trial history is the cause, then what is it about the trial history that is causing haptic and non-haptic grasps to differ for slopes?

Looking at the RNK condition for a single participant, we recall that a set of trial orders for this condition comprises 36 trials, half of which are haptic trials and half of which are non-haptic trials. This excludes the possibility that an imbalance of trials of one type or the other is responsible for the effect, since there are equal numbers of haptic and non-haptic trials. But ensuring equal prevalence of haptic and non-haptic trials in the RNK condition, and ensuring that the condition was sufficiently ‘randomized’, required the imposition of certain constraints during trial-order generation. Namely, that there be equal numbers of haptic and non-haptic trials, and that not more than 3 haptic or 3 non-haptic trials be presented consecutively. These constraints meant that the trial orders were actually pseudo-randomized, and not truly randomized, which led to the emergence of a fascinating pattern at the heart of our anomalous result.

When the trials in the RNK condition were grouped *not by* individual trial type, but by *pairs* of trials, a pattern emerged. First, let us clarify that for a set of 36 trials there are 35 pairs of trials (if you include overlapping pairs), and that there are four types of trial pairs which fall into two groups: 1*a*. haptic / non-haptic (1/0); 1*b*. non-haptic / haptic (0/1); 2*a*. haptic / haptic (1/1); 2*b*. non-haptic / non-haptic (0/0). Collectively, let us refer to 1/0 trial-pairs and 0/1 trial pairs as ‘switching’ trial pairs, and 1/1 trial pairs and 0/0 trial pairs as ‘same’ trial pairs. It emerged that ‘switching’ trial pairs occurred with approximately twice the frequency as ‘same’ trial pairs, meaning that on any given trial *n*, trial *n*+1 was approximately *twice as likely* to be a trial of the opposite type (in terms of haptic feedback) as the current trial. Another way of thinking about this is regarding our RNK condition as a weak Alternating condition in which the participants do not have knowledge of upcoming haptic feedback (as they would do in a pure Alternating condition). See Appendix H for a table summarizing the frequencies of trial-pairs across all 30 participants.

Knowing that (all other things being equal) the current trial is most heavily influenced by the past trial, and the past trial is more likely to be of the opposite type of trial as the current trial, we may now explain the phenomenon we see between haptic and non-haptic grasps in our RNK condition. Suppose the current trial is a haptic trial – the visuomotor system doesn’t know that it is a haptic trial during the grasp, but once it touches the object at the end of the grasp, it stores this information, and then it prepares for the next trial. In preparation for the next trial, the greatest influence on grip scaling (all other things being equal) is the previous trial, which was a haptic grasp – so the visuomotor system prepares to perform this next grasp *more like a haptic grasp*, because that is the most recent experience. Of course, this next trial is now more likely to be a non-haptic trial, but the system won’t know this until the end of the grasp, and so it performs the grasp on this next (probably non-haptic) trial, and the grasp looks more like a haptic grasp than a non-haptic grasp. The system then reaches the end of the grasp, and discovers no object, and now it prepares for the next trial, which it will treat *more like a non-haptic grasp*, despite the fact that the next trial is more likely to be a haptic trial. If this is indeed what is occurring, then we would expect to see a ‘reversal’ of slopes values between haptic and non-haptic grasps in the RNK condition, and this is exactly what we find. Whereas haptic slopes are much *less* steep than non-haptic slopes in the blocked condition, the reverse is true in the RNK condition – haptic slopes are significantly steeper than non-haptic slopes in the RNK condition, which we suggest is resulting from a trial history effect of haptic feedback, emerging from the pseudo-randomization of the trial orders due to the constraints we imposed (see Figure 6).

We conclude our discussion of this highly surprising result by recognizing that there are obviously limitations of drawing inferences about the mechanism behind this effect from this one finding alone. Further research is required to characterize the nature and the extent of any trial history effects of haptic feedback on dorsal-stream mediated grasping in the absence of knowledge of upcoming haptic feedback.

Limitations

One obvious limitation of our study that follows from the previous discussion of trial history effects is the fact that pseudo-randomization led to biases in recent haptic feedback that were strong enough to emerge as a distinct significant effect. Although not strictly a limitation of the study design, the constraints we imposed did appear to limit the consistency of our findings across dependent variables, and somewhat reduced the strength of our arguments. Future studies should take the trial history effect into account, and either attempt to control for it, or attempt to quantify it so it can be included in the model when making hypotheses.

Another potentially significant limitation of our experiment was that participants who had the RK condition immediately preceding, or even just some-time preceding, the RNK condition, may have ascertained that the sequence of trials was identical across the two conditions, and may have remembered salient pairs of trials or a unique string of trials from the RK condition, compromising the integrity of the RNK condition. However, it seems unlikely that such a strategy so evidently counter to the aims of the experiment was prevalent, in part because of the 'good-subject effect'. Moreover, even if they had employed such a strategy, we suspect that participants would not have been able to accurately recall many trials, due to memory constraints. Nonetheless, this limitation bears some consideration given the number of participants for whom this strategy was available: exactly half of the total 30 participants received the RK condition some-time before the RNK condition, of which seven participants received the RK condition immediately preceding the RNK condition. In addition, the conjecture that such a strategy was employed by at least *some* participants is strengthened by the experimenter's notes post data-collection, which indicate that two participants (while responding to the question of whether they felt they had been able to predict any trials in the RNK condition) reported that during the RNK condition they had concluded that the trial order was the same as for the RK condition, and had subsequently treated the RNK condition "like a game" in which they tried to remember upcoming trials. The use of memory strategies notwithstanding, we believe that attempts at predicting upcoming trials in the RNK condition were generally unsuccessful, as data from the RNK condition for participants who reported feeling that they had been able to predict upcoming trials did not appear to differ, upon trial-by-trial visual inspection of grasp kinematics, from data for participants who explicitly reported having felt that they could not predict upcoming trials.

Future Research

An interesting question remains regarding the frequency of intermittent haptic feedback required to provoke dorsal-stream grasping, in the absence of knowledge of upcoming haptic feedback. In our RNK condition, haptic and non-haptic trials occurred with equal frequency, so the participant could be quite confident that ‘lazy’ grasping would have undesirable consequences. Future research could explore the parameters associated with provoking the more cautious dorsal-stream response by varying the number of sparse haptic grasps interspersed between more numerous non-haptic grasps, in a condition where there is no knowledge of upcoming haptic feedback.

Other avenues for research include pursuing the reasons behind why our Alternating condition (ALT), which we excluded from analyses, appeared similar to our RK condition. It seems likely that the similarity stems from the visuomotor system not having access to the knowledge of upcoming haptic feedback that would allow it to differentiate between the ALT and RK conditions – in essence, the cognitive inaccessibility of the dorsal stream we discussed earlier – similar to Whitwell *et al*.’s (2008) finding that the dorsal stream doesn’t have access to knowledge of upcoming *visual* feedback when programming future grasps. However, because we did not analyze our ALT data, we cannot say that our cursory comparison between the ALT and RK conditions provides support for this conclusion. Further research could explore the extent to which a purely alternating condition and randomized conditions of varying formats differ, for grasps made when there is knowledge of upcoming haptic feedback.

Conclusions

Our study draws four conclusions from our data, based upon our three hypotheses and upon our novel finding of a probable trial-history effect acting on the dorsal-stream mediated grasps of the RNK condition. Firstly, we found that when controlling for knowledge, as in our RK condition, interleaving haptic and non-haptic trials did not normalize prehension for the non-haptic grasps. These findings support our contention that it was the absence of knowledge of upcoming haptic feedback, rather than the intermittent haptic feedback, which was responsible for the 'natural prehension' observed by Bingham *et al*. in their 2007 study. Secondly, we found that pantomime grasps were susceptible to the influence of knowledge of upcoming haptic feedback, whereas normal grasps were not – insofar as pantomime grasps refer to ventral-stream mediated grasps (that is, non-haptic grasps when there is knowledge of upcoming haptic feedback), and normal grasps refer to dorsal-stream mediated grasps. These findings are consistent with a large body of literature suggesting that the ventral stream is cognitively accessible, whereas the dorsal stream is cognitively inaccessible. We also found evidence to support the idea that in the absence of knowledge of upcoming haptic feedback, grasps are mediated by the dorsal stream. Thirdly, we found that pantomime grasps showed the expected decrements in precision and differences in kinematic variables compared to normal grasps. Lastly, the emergence of a significant difference between slopes values for haptic and non-haptic grasps in our RNK condition provides evidence that the dorsal stream is largely influenced by recent proprioceptive and tactile events. The fact that for slopes, dorsal-stream grasps were influenced by this effect but not by the manipulation of knowledge of upcoming haptic feedback further supports the idea that the dorsal stream is a cognitively impenetrable system specialized for visually-guided grasping, as proposed by the Two Visual Systems Hypothesis.

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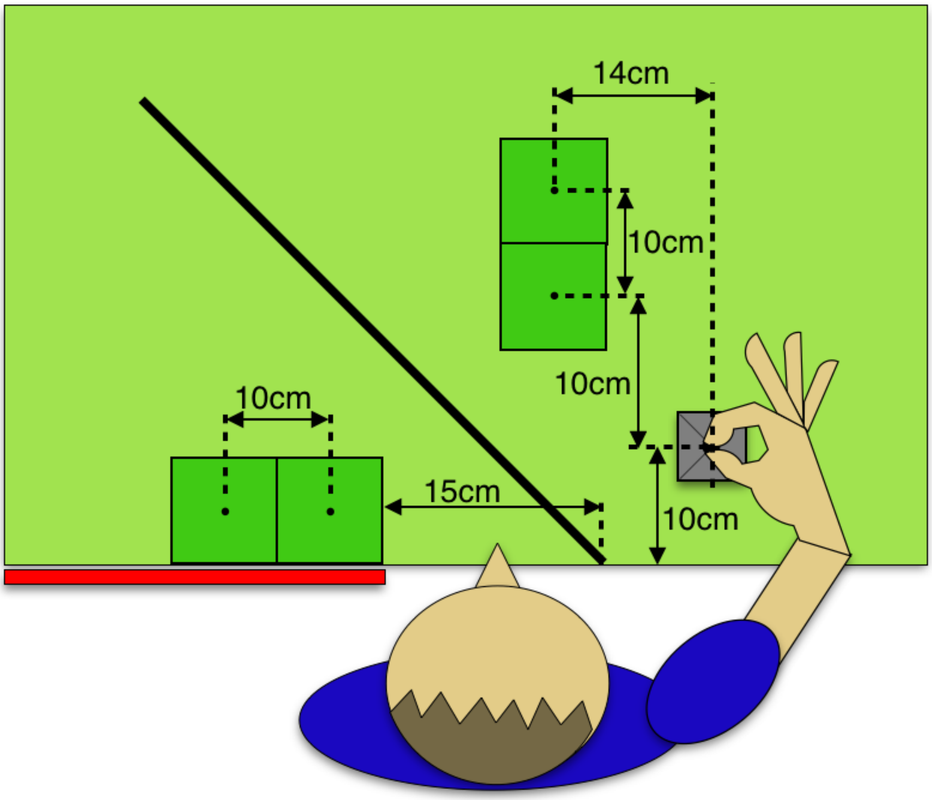
Appendix A

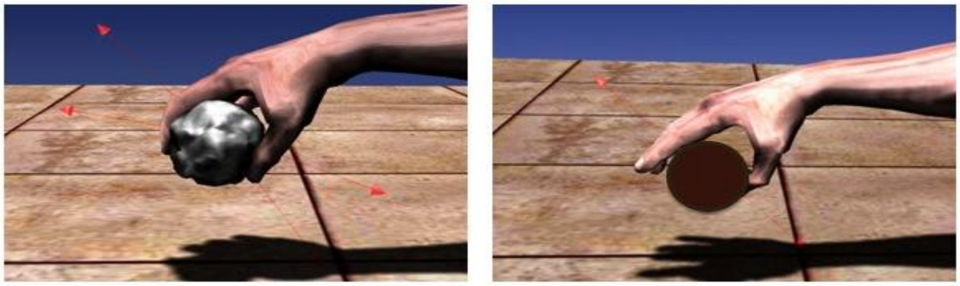


Note. Top-down view of the mirror-apparatus. A mirror (thick black line) was positioned at a 45° angle to the edge of the table, with the reflecting surface facing the participant. Four thin wooden square platforms (dark green squares) each with a raised pin in the center were secured to the table at the mirror-symmetrical positions shown; a hole on the bottom surface of each object accommodated the raised pin on the platforms, allowing the objects to be placed centrally on every trial. An opaque board (thick red line) was secured vertically to the edge of the table closest to the participant, occluding direct view of objects placed in front of the mirror. The start button (grey square) was secured to the table 14cm to the right of and 10cm closer to the participant than the nearest object position. The object reflected in the mirror produced a virtual image behind the mirror towards which the participant aimed their grasp. Placing an object in front of the mirror, and an identical object at the mirror-symmetrical position behind the mirror, provided haptic feedback to the grasp. Placing an object only in front of the mirror permitted grasps to be directed at a visually-presented object while denying haptic feedback; that is, an object could be seen at the location behind the mirror but could not be grasped at that location. A similar setup as shown here was used by Bingham *et al*. (2007) in their study.

Appendix B

PARTICIPANTS ARE NEEDED!!

Grasping experiment for Psychology



The experiment involves grasping wooden objects of different sizes and lasts approximately 45 minutes. Qualified individuals (**Right-handed individuals with normal or corrected-to-normal vision)** will receive $10 for participating.

If you are interested in participating please email your contact information to: **grasp_experiment@hotmail.com**

grasp_experiment@hotmail.com
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Appendix C

LETTER OF INFORMATION FOR BEHAVIOURAL PARTICIPANTS

The Neural Substrates of Visual Perception and Visually-Guided Action

Principal Investigator:
Melvyn A. Goodale, Ph.D., F.R.S.C.
Department of Psychology
The University of Western Ontario, London, ON
Telephone: (519) 661-2070
E-mail: mgoodale@uwo.ca

Introduction

You are being invited to participate in a research study to determine which regions of the brain are involved when people perceive objects and act towards them. This letter contains information to help you decide whether or not to participate in this research study. It is important for you to understand why the study is being conducted and what it will involve. Please take the time to read this carefully and feel free to ask questions if anything is unclear or there are words or phrases you do not understand.

Research Procedures

If you agree to take part in this study, we will be recording your responses to visual targets. In some cases you may be shown lights or patterns and asked to report what you see. In other cases, you may be asked to reach toward and pick up an object or touch a small target. Small infrared lights (approximately 1/8" or .25 cm.) will be attached with adhesive tape to two of your fingers and your wrist. Cameras sensitive to infrared light will follow the movement of the hand and arm. In addition, your eye movements and pupil size will be recorded by shining an invisible infrared light onto your eyes and recording the reflection. Information about your responses and movements will be stored as numbers in a computer. The test session will last one to two hours. There will be opportunities to rest during testing.

Voluntary Participation

Participation in this study is voluntary. You may refuse to participate, refuse to answer questions or withdraw from the study at any time with no effect on your status as a patient or your future medical care.

Compensation

You will be compensated $10 to cover your time, parking and the inconveniences associated with participating in the study.

Benefits

While this study will not result in any direct benefit to you, it may help clinicians understand how the brain uses visual information and therefore be of some benefit to patients in the future.

Risks

There are no known risks to your participation in this study.

Confidentiality

Any information obtained from this study will be kept confidential. In order to understand the data collected from the testing in this study, copies of some of the information from your medical record will be taken to the University of Western Ontario, Department of Psychology. The information may include results from MRI scans taken for clinical care, copies of the MRI images themselves and data regarding your treatment in the hospital. We will try to de-identify this data as much as possible, however some of the information may be identifiable. This information will be stored on a secure computer which will be accessible only to persons involved in the study. In the event of publication, any data resulting from your participation will be identified only by case number, without any reference to your name or personal information. The data will be stored on a secure computer in a locked room. Both the computer and the room will be accessible only to the experimenters. After completion of the experiment, data will be archived on storage disks and stored in a locked room for five years, after which they will be destroyed.

Representatives of the University of Western Ontario Health Sciences Research Ethics Board may require access to your study-related records or may follow up with you to monitor the conduct of the study.

Estimate of participant's time and number of participants

Each experiment will last approximately 45 minutes. The entire research project will involve approximately 500 subjects.

Contact Information

If you would like to receive a copy of the overall results of the study, of if you have any questions about the study please feel free to contact the Principal Investigator at the contact information provided above.

If you have any questions about your rights as a research participant or the conduct of the study you may contact:

The Office of Research Ethics
The University of Western Ontario
519-661-3036
E-mail: ethics@uwo.ca
Review# 06882E (Behavioural)

You do not waive any legal rights by signing the consent form. You will be provided with a copy of this letter of information and the consent form.

Appendix D

Page 3 of 3

CONSENT FOR BEHAVIOURAL RESEARCH STUDY

The Neural Substrates of Visual Perception and Visually-Guided Action

You do not waive any legal rights by signing the consent form. You will be provided with a copy of this letter of information and the consent form.

I have read the letter of information, have had the nature of the study explained to me and I agree to participate. All questions have been answered to my satisfaction.

Dated in ____________________, this__________ day of________________,20_____.

Name of Participant (Please print)	Name of Principal Investigator:
Signature of Participant:	Signature of Principal Investigator:

Name of Person Responsible for Obtaining Consent: ______________________________

(Please print)

Signature of Person Responsible for Obtaining Consent: ______________________________

Dated in ____________________, this__________ day of________________,20_____.

Participant's Initials: ______

Appendix E

1-Random With Knowledge

Trial No	Object	Position	Haptic	
1	2	2	0	☐
2	3	2	1	☐
3	3	1	1	☐
4	1	2	0	☐
5	2	2	1	☐
6	1	1	0	☐
7	2	1	0	☐
8	1	2	1	☐
9	1	1	1	☐
10	3	1	0	☐
11	3	2	0	☐
12	2	1	1	☐
13	3	2	1	☐
14	1	1	0	☐
15	2	2	1	☐
16	2	1	0	☐
17	1	2	1	☐
18	3	2	0	☐
19	3	1	1	☐
20	1	1	1	☐
21	2	2	0	☐
22	3	1	0	☐
23	2	1	1	☐
24	1	2	0	☐
25	1	2	1	☐
26	2	1	1	☐
27	1	1	0	☐
28	2	2	1	☐
29	2	1	0	☐
30	1	2	0	☐
31	3	1	1	☐
32	3	2	0	☐
33	1	1	1	☐
34	2	2	0	☐

35	3	1	0	☐
36	3	2	1	☐

2-Alternating

Trial No	Object	Position	Haptic	
37	1	2	0	☐
38	1	1	1	☐
39	3	1	0	☐
40	3	2	1	☐
41	1	1	0	☐
42	2	2	1	☐
43	2	2	0	☐
44	3	1	1	☐
45	3	2	0	☐
46	1	2	1	☐
47	2	1	0	☐
48	2	1	1	☐
49	3	2	0	☐
50	1	2	1	☐
51	3	1	0	☐
52	1	1	1	☐
53	2	2	0	☐
54	3	1	1	☐
55	1	2	0	☐
56	2	2	1	☐
57	2	1	0	☐
58	3	2	1	☐
59	1	1	0	☐
60	2	1	1	☐
61	2	2	0	☐
62	1	2	1	☐
63	2	1	0	☐
64	1	1	1	☐
65	1	2	0	☐
66	3	2	1	☐
67	3	1	0	☐
68	2	2	1	☐
69	1	1	0	☐

70	2	1	1	☐
71	3	2	0	☐
72	3	1	1	☐

3-Random NO Knowledge

Trial No	Object	Position	Haptic	
73	2	2	0	☐
74	3	2	1	☐
75	3	1	1	☐
76	1	2	0	☐
77	2	2	1	☐
78	1	1	0	☐
79	2	1	0	☐
80	1	2	1	☐
81	1	1	1	☐
82	3	1	0	☐
83	3	2	0	☐
84	2	1	1	☐
85	3	2	1	☐
86	1	1	0	☐
87	2	2	1	☐
88	2	1	0	☐
89	1	2	1	☐
90	3	2	0	☐
91	3	1	1	☐
92	1	1	1	☐
93	2	2	0	☐
94	3	1	0	☐
95	2	1	1	☐
96	1	2	0	☐
97	1	2	1	☐
98	2	1	1	☐
99	1	1	0	☐
100	2	2	1	☐
101	2	1	0	☐
102	1	2	0	☐

103	3	1	1	☐
104	3	2	0	☐
105	1	1	1	☐
106	2	2	0	☐
107	3	1	0	☐
108	3	2	1	☐

4-Block Non-Haptic

Trial No	Object	Position	
109	2	1	☐
110	1	2	☐
111	1	1	☐
112	2	2	☐
113	1	2	☐
114	3	1	☐
115	2	1	☐
116	3	2	☐
117	3	1	☐
118	2	2	☐
119	3	2	☐
120	1	1	☐
121	2	2	☐
122	1	1	☐
123	1	2	☐
124	3	1	☐
125	2	1	☐
126	3	2	☐

5-Block Haptic

Trial No	Object	Position	
127	2	1	☐
128	1	2	☐
129	1	1	☐
130	2	2	☐
131	1	2	☐
132	3	1	☐
133	2	1	☐
134	3	2	☐
135	3	1	☐
136	2	2	☐
137	3	2	☐
138	1	1	☐
139	2	2	☐
140	1	1	☐
141	1	2	☐
142	3	1	☐
143	2	1	☐
144	3	2	☐

Appendix F

Table 1

Reaction Time (RT) values by Presentation and Haptic Feedback

	Presentation Condition		
	Blocked	Randomized	Difference
Haptic Trials	613.71 (34.12)	623.40 (29.32)	9.69
Non-Haptic Trials	736.20 (39.80)	684.72 (32.58)	- 51.48
Difference	122.49**	61.32**	

Note. Mean values for reaction time, in ms, with standard error displayed in brackets.

Asterisks indicate the difference is significant at: *$p < .012$; **$p \leq .001$

Table 2

Reaction Time (RT) values by Knowledge and Haptic Feedback

	Knowledge of Upcoming Haptic Feedback		
	Yes	No	Difference
Haptic Trials	623.40 (29.32)	732.78 (37.79)	109.38**
Non-Haptic Trials	684.72 (32.58)	720.53 (36.96)	35.81
Difference	61.32**	- 12.25	

Note. Mean values for reaction time, in ms, with standard error displayed in brackets.

Asterisks indicate the difference is significant at: *$p < .012$; **$p \leq .001$

Table 3

Final Grip Aperture (FGA) values by Presentation and Haptic Feedback

	Presentation Condition		
	Blocked	Randomized	Difference
Haptic Trials	62.22 (0.49)	62.10 (0.45)	- 0.12
Non-Haptic Trials	55.96 (1.31)	56.31 (1.28)	0.35
Difference	- 6.26**	- 5.79**	

Note. Mean values for final grip aperture, in mm, with standard error displayed in brackets.

Asterisks indicate the difference is significant at: *$p < .012$; **$p \leq .001$

Table 4

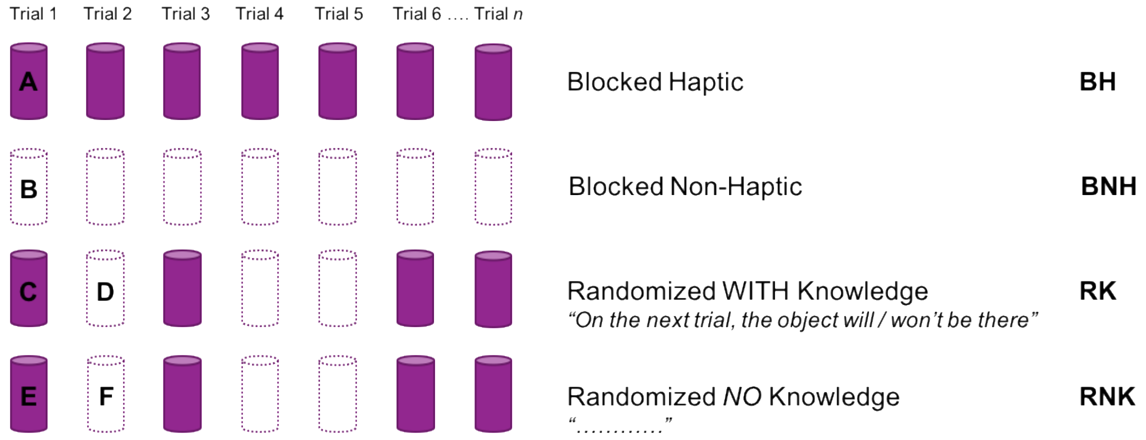
Final Grip Aperture (FGA) values by Knowledge and Haptic Feedback

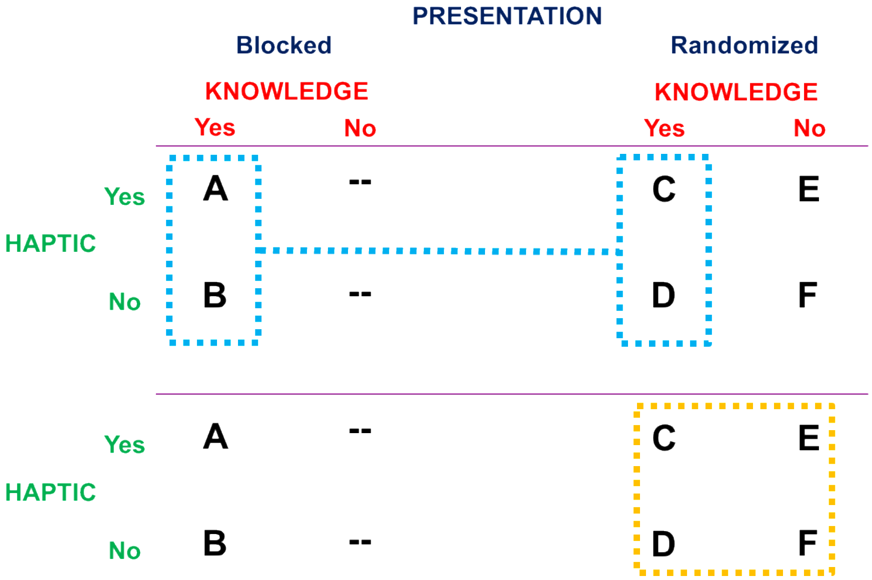
	Knowledge of Upcoming Haptic Feedback		
	Yes	No	Difference
Haptic Trials	62.10 (0.45)	61.62 (0.44)	- 0.48
Non-Haptic Trials	56.31 (1.28)	52.91 (1.50)	- 3.40*
Difference	- 5.79**	- 8.71**	

Note. Mean values for final grip aperture, in mm, with standard error displayed in brackets.

Asterisks indicate the difference is significant at: *$p < .012$; **$p \leq .001$

Appendix G





The above diagrams provide a schematic representation of the two ANOVA procedures performed on each dependent variable. For each dependent variable, the first analysis is encapsulated by the BLUE box: trials from the blocked haptic condition (A) and the blocked non-haptic condition (B), were compared to haptic trials (C) and non-haptic trials (D) from the random with knowledge condition. The second analysis is encapsulated by the YELLOW box: haptic trials (C) and non-haptic trials (D) from the random with knowledge condition, were compared to haptic trials (E) and non-haptic trials (F) from the random *no* knowledge condition.

This schematic also illustrates why two ANOVAs were necessary. The existence of two pseudo-conditions (represented by the black dashes) precluded direct comparison across conditions. These conditions are pseudo-conditions (conditions that cannot exist) because it is not possible to have a blocked condition in which the participant has *no* knowledge of upcoming haptic feedback. That is, when a condition involves consecutive trials of the same type, for example serial haptic trials, then a participant cannot be kept from knowing that future trials will provide haptic feedback.

Appendix H

Table 1

Frequencies of Trial-Pairs in the Random No Knowledge Condition, Across All Subjects

Subject	Trial-Pair Types				Skewedness
	0 / 0	1 / 0	0 / 1	1 / 1	
1	8	10	11	6	0.60
2	6	12	11	6	0.66
3	6	11	12	6	0.66
4	6	11	12	6	0.66
5	7	10	11	7	0.60
6	5	13	13	4	0.74
7	7	10	11	7	0.60
8	7	11	10	7	0.60
9	5	12	11	7	0.66
10	5	13	12	5	0.71
11	5	12	13	5	0.71
12	7	10	11	7	0.60
13	6	12	12	5	0.69
14	7	11	10	7	0.60
15	6	11	12	6	0.66
16	8	10	10	7	0.57
17	5	12	13	5	0.71
18	7	11	11	6	0.63
19	6	12	12	5	0.69
20	4	13	13	5	0.74
21	4	13	13	5	0.74
22	5	12	13	5	0.71

23	5	12	13	5	0.71
24	8	9	10	8	0.54
25	8	9	10	8	0.54
26	6	12	12	5	0.69
27	6	11	11	7	0.63
28	4	13	14	4	0.77
29	6	11	12	6	0.66
30	8	10	10	7	0.57
MEANS:	**6.10**	**11.33**	**11.63**	**5.97**	**0.66**

Note. 1 = haptic trial; 0 = non-haptic trial. Skewedness = sum of (1/0) + (0/1) trials / 35.